

# Chapter 1

## First Ornithischian and Theropod Dinosaur Teeth from the Middle Jurassic Kota Formation of India: Paleobiogeographic Relationships

Guntupalli V. R. Prasad and Varun Parmar

**Abstract** The Middle Jurassic Kota Formation of the Pranhita-Godavari Valley in peninsular India is well known for its vertebrate fauna comprising fishes, sphenodontians, iguanian lizards, cryptodire turtle, crocodilians, pterosaurs, sauropod dinosaurs and early mammals. However, no theropod and undoubted ornithischian dinosaur remains have been reported from the Jurassic of India until now. Here we describe the first theropod dinosaur teeth representing five morphotypes of Dromaeosauridae, one *Richardoestesia*-like form, and one Theropoda indet. The ornithischian dinosaur teeth are described under five morphotypes of Ornithischia indet. The new dinosaur fauna improves the diversity of the Jurassic vertebrate fauna of India significantly. It also improves the impoverished Jurassic record of dromaeosaurid and primitive ornithischian dinosaurs of the Gondwana. At higher taxonomic levels, the Kota fauna demonstrates close compositional similarities with Laurasian Jurassic faunas, such as the Middle Jurassic fauna of England, and limited Gondwanan affinities, which may suggest closer connection with the Laurasian continents and existence of some biogeographic partitioning within the Gondwana in the Jurassic. However, this interpretation is subject to further verification in the least explored areas of Gondwana.

**Keywords** Ornithischia • Dromaeosauridae • Vertebrate • Jurassic • Pranhita-Godavari • Gondwana • Laurasia

## Introduction

In India, continental Jurassic sequences are represented by the Lower Jurassic Lathi Formation of western India and the Middle Jurassic Kota Formation of the Pranhita-Godavari Valley, southcentral India. Plant, invertebrate, vertebrate, and trace fossils including theropod footprints have been reported from the Lathi Formation (Pieńkowski et al. 2015). Conversely, the Kota Formation, has been an important source of vertebrate fossils over the past three decades and since the first reports of fish fossils by Egerton (1851, 1878), many groups of vertebrates have been documented. These include: fish, such as *Lissodus indicus* (Yadagiri 1986; Prasad et al. 2004), ?*Polyacrodus* sp. (Prasad et al. 2004), *Tetragonolepis oldhami* (Egerton 1878; Jain 1973), *Paradapedium egertoni* (Jain 1973), *Indocoelacanthus robustus* (Jain 1974a), *Lepidotes deccanensis* (Sykes 1851; Jain 1983), *Pholidophorus kingi*, *P. indicus* (Yadagiri and Prasad 1977), reptiles, including the sphenodontians *Rebbanasaurus jaini* and *Godavrisaurus lateefi* (Evans et al. 2001), the iguanian lizard *Bharatagama rebbanensis* (Evans et al. 2002), teleosaurid crocodiles (Owen 1852; Nath et al. 2002), the cryptodire turtle *Indochelys spatulata* (Datta et al. 2000), atroposaurid crocodiles, the pterosaurs *Campylognathoides indicus* (Jain 1974b) and *Rhamphorhynchus* sp. (Rao and Shah 1963), and the sauropod dinosaurs *Barapasaurus tagorei* (Jain et al. 1975; Bandyopadhyay et al. 2010) and *Kotasaurus yamanapalliensis* (Yadagiri et al. 1979; Yadagiri 2001), and mammals *Kotatherium haldeni* (Datta 1981), *Trishulotherium kotaensis*, *Indotherium pranhitai* (Yadagiri 1984; Prasad and Manhas 2002 [= *Indozostrodon simpsoni* Datta and Das 2001]), *Nakunodon paikasiensis* (Yadagiri 1985), *Paikasigudodon yadagirii* (Prasad and Manhas 1997, 2002), *Dyskritodon indicus* (Prasad and Manhas 2002), *Gondtherium dattai* (Prasad and Manhas 2001, 2007), *Indobaatar zofiae* (Parmar et al. 2013) and an australosphenidan (Parmar et al. 2015; Prasad et al.

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2015). It is apparent from this faunal list that the Kota Formation dinosaurs have been represented only by basal sauropods thus far. Theropods and ornithischians have been conspicuously absent from the Kota vertebrate fauna. In recent years, the Kota Formation has been explored extensively for Jurassic mammals (Prasad and Manhas 1997, 2002, 2007; Datta and Das 2001; Parmar et al. 2013). Bulk samples (7000 kg) from mammal yielding horizons were screen-washed in search of micromammals, which led to the recovery of many isolated teeth of crocodiles, pterosaurs, ornithischians and theropods. In view of the rarity of archosaur fossils from the Indian Jurassic, any new find is of great significance in terms of faunal diversity. In this paper, the ornithischian and theropod teeth are described and their paleobiogeographic significance is discussed.

## Geological Setting

The Pranhita-Godavari (P-G) Valley in Telangana state, India preserves an almost uninterrupted sequence of continental Gondwana Supergroup of rocks ranging in age from Early Permian to Early Cretaceous. The Upper Gondwana Group exposed in this valley are of special significance as they provide an excellent opportunity to document the rare Mesozoic terrestrial ecosystems from South Asia. These rocks are exposed in a NW-SE trending fault bounded linear belts. In the beginning, vertebrate yielding Upper Triassic – Lower Jurassic strata of the P-G Valley were referred to as the Kota-Maleri beds (Hughes 1876). Later, King (1881) separated the Kota-Maleri beds into two distinct stratigraphic units, the lower Maleri beds containing a Late Triassic fauna and the overlying Kota beds yielding an Early Jurassic fauna. Following extensive field mapping, Kutty (1969) revised the Upper Gondwana stratigraphy of the P-G Valley and subdivided the Upper Gondwana Group into the lower Middle Triassic Yerrapalli Formation, upper Middle Triassic Bhimaram Sandstone, lower Upper Triassic Maleri Formation, Upper Triassic – Lower Jurassic Dharmaram Formation, Lower Jurassic Kota Formation, and Lower Cretaceous Gangapur Formation (Kutty et al. 1987). The Triassic Yerrapalli, Maleri and Dharmaram formations are red clay dominated sequences with subordinate sandstones and lime-pellet rocks, and the Bhimaram Sandstone Formation is predominantly represented by coarse sandstones. The Gangapur Formation, which overlies the Kota Formation with an angular unconformity, is a sequence of coarse sandstones and alternating sandstones, mudstones and silty mudstones (Kutty et al. 1987).

The Kota Formation succeeds the topmost red clay band of the Dharmaram Formation with a coarse pebbly sandstone that becomes thick and conglomeratic towards the eastern

part of the basin. The conglomerate bed, together with an abrupt change in the fauna from that of the underlying Dharmaram Formation, was taken as evidence for a minor break in sedimentation (Kutty et al. 1987). The Kota Formation, with its type section exposed near the village Kota in Sironcha district, Maharashtra on the left bank of the Pranhita river, approximately 8 km north of its confluence with the Godavari river, is lithologically divided into lower and upper units (Rudra 1982). The lower unit comprises coarse, hard, compact and pebbly sandstone that grades upwards into fine-grained white sandstone, red and green clays, mudstones and siltstones. The dinosaur and mammal-yielding mudstones and siltstones of the lower unit are succeeded by the calcareous shale and limestones of the upper unit. The limestone is overlain by mudstones and ferruginous shale interbedded with sandstone. The clay - mudstone - siltstone sequence of the lower unit produced sauropod dinosaurs, mammals, ostracods and charophytes, whereas the limestone-bearing upper unit yielded articulated fish skeletons, a teleosaurid crocodylomorph, sphenodontians, iguanian lizards, a cryptodiran turtle, mammals and ostracods (Bandyopadhyay and Roychowdhury 1996; Parmar et al. 2013).

Rudra (1982) interpreted the lower unit of the Kota Formation as a fining upward sequence deposited by a laterally shifting meandering river system, while the upper unit is a coarsening upward sequence deposited in a braided river system. The limestone facies of the upper part was considered to have been deposited in a distal playa-type system of interconnected lakes (Rudra 1982; Rudra and Maulik 1987). The faunal and floral elements of the Kota Formation also indicate freshwater lacustrine depositional environment (King 1881; Robinson 1970; Tasch et al. 1973; Govindan 1975; Jain 1980, 1983; Jain and Roy Chowdhury 1987; Rudra and Maulik 1987; Feist et al. 1991; Bhattacharya et al. 1994).

## Age

Based on the fishes *Paradapedium egertoni*, which was considered similar to Early Jurassic *Dapedium* of Europe, *Tetragonolepis oldhami* (considered morphologically close to *Tetragonolepis* of Upper Liassic of Europe [Jain 1973]), and *Lepidotes deccanensis* (that shares affinities with Upper Liassic [Toarcian] *Lepidotes elevensis* from Europe), the Kota Formation has been assigned an Early Jurassic (Liassic) age (Jain 1980, 1983). A similar age was suggested by Yadagiri and Prasad (1977) on the basis of the pholidophorid fishes, *Pholidophorus kingi* and *P. indicus*. Palynofossils (Prabhakar 1989) and charophytes (Bhattacharya et al. 1994) also indicate an Early Jurassic age. However, freshwater ostracods, represented by *Darwinula* cf. *D. sarytirmensis*

and *Timiriasevia*, have been used to infer a Middle Jurassic age for the Kota Formation (Govindan 1975). Vijaya and Prasad (2001) assigned a younger Middle – Upper Jurassic age based on a palynological study. Contrary to these later, younger, age assignments, Evans et al. (2001) regarded the Early Jurassic age as more likely because the dental morphology of the two Kota sphenodontian taxa, *Rebbanasaurus* and *Godavarisaurus*, is more derived than those of the basal rhynchocephalians *Diphydontosaurus* and *Planocephalosaurus* of Late Triassic age, and *Gephyrosaurus* of Early Jurassic age. The current study reveals the presence of ornithischian and theropod teeth in association with a vertebrate microfossil assemblage compositionally similar to that of Middle Jurassic of UK pointing to a potentially younger Middle Jurassic age for the Kota Formation.

## Methods and Materials

### Locality Information

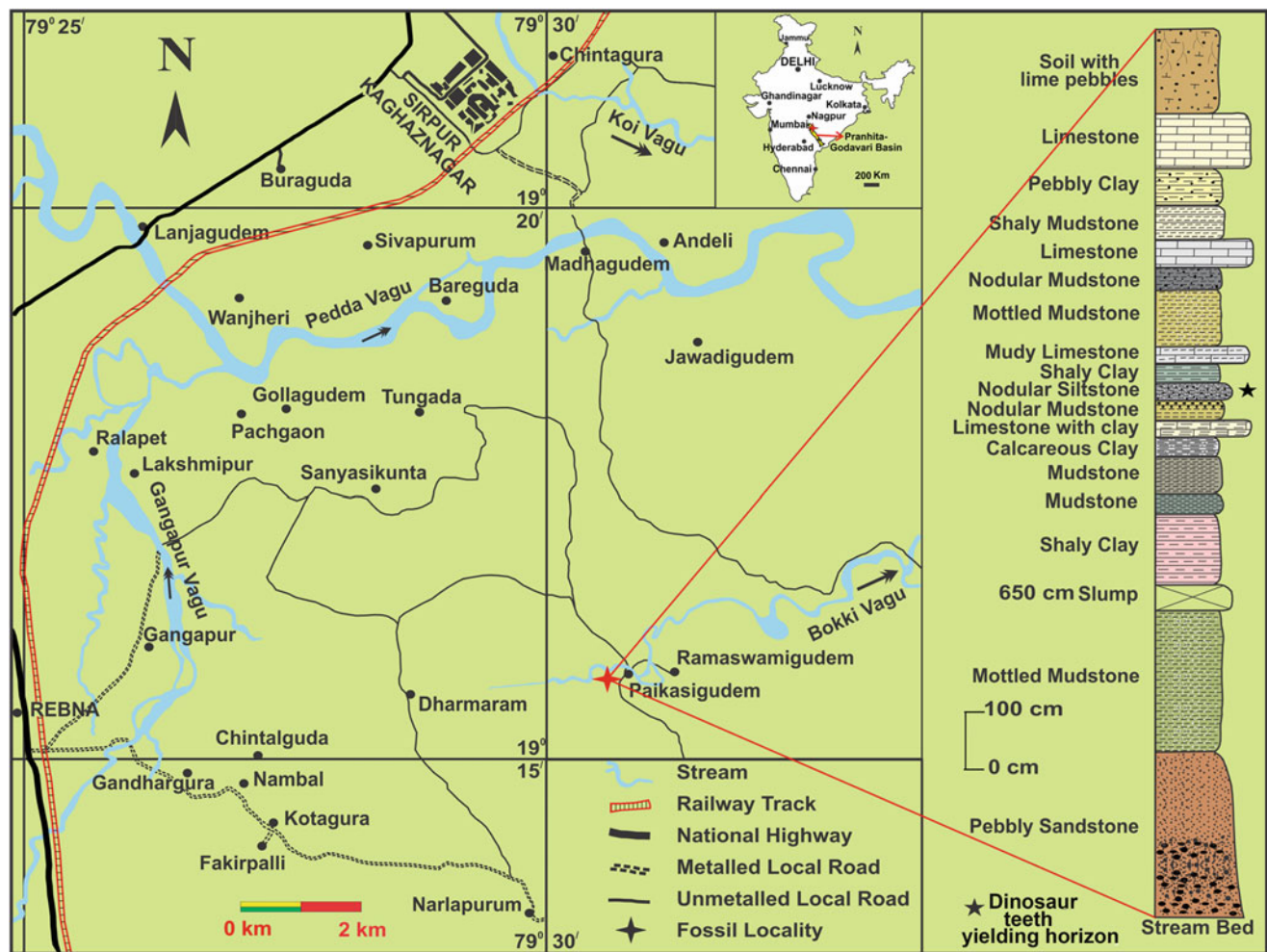
The Kota Formation outcrop yielding the dinosaur teeth described herein is a localized section with a short lateral extent as is the case with most known sections of this formation. The outcrop is a small cliff exposed along a stream channel 300 m southwest of Paikasigudem village, Rebbana Mandalam, Adilabad district, Telangana, India (Fig. 1.1). The measured lithological section consists of 20 m of sandstones, clays, mudstones and siltstones with two distinctive limestone and two impure thin limestone bands (Fig. 1.1, 1.2). The dinosaur teeth are derived from a 27 cm thick greenish-grey nodular siltstone situated about 9.5 m above the base of the section representing Rudra's (1982) upper unit of the Kota Formation. Between 1997 and 2013 about 7000 kg of this siltstone were subjected to screen-washing in search of early mammals. As the siltstones are relatively soft, the combined use of kerosene and water was employed to disaggregate the rock matrix.

### Fossils Collected

The residue left after screen-washing was sorted under the microscope for vertebrate microfossils which led to the recovery of more than 5000 specimens of vertebrate fossils predominantly represented by fish teeth and scales in addition to jaw fragments of sphenodontians and iguanian lizards, crocodilian, few pterosaur and dinosaur teeth, and 50 mammalian teeth. The fossil-bearing horizon is also highly enriched in ostracod carapaces. The vertebrate microfossils are very well-preserved except for damage related to mechanical breakage which could be pre- or post-burial or

due to breakage during screen-washing. No substantial rounding of bones and teeth is observed which implies that the specimens have not undergone extensive transportation. The dinosaur teeth are represented mainly by crowns possibly due to resorption of the root during tooth replacement as is evident from the presence of resorption pits at the crown base. The presence of wear facets on tooth apices and loss of denticles also attest to tooth use. The dinosaur fauna described here is represented by 71 theropod and 35 ornithischian teeth. Photographs of the described teeth were taken with Leica S8APO Stereoscopic Binocular Microscope attached with Leica MC 120 HD Digital Camera and Zeiss Scanning Electron Microscope and Zeiss EVOMA 10 Scanning Electron Microscope.

The utility of isolated dinosaur teeth in identification, at least at family level and above, has been demonstrated by Currie et al. (1990), Farlow et al. (1991), Basso (1997), Smith et al. (2005), Larson and Currie (2013), Hendrickx and Mateus (2014) and Gerke and Wings (2016) for theropod and Coombs (1990), Parkar et al. (2005), Butler et al. (2006), Irmis et al. (2007) for ornithischian dinosaurs. Tooth measurements were made using the methods of Currie et al. (1990), Farlow et al. (1991) and Smith et al. (2005) for theropod teeth. In addition to fore-aft basal length (FABL), basal labiolingual width (BW), total apico-basal height of the crown (TCH) perpendicular to FABL proposed by Currie et al. (1990), the denticle size difference index (DSDI) of Rauhut and Werner (1995), involving the measurement of the ratio of the number of denticles per given length unit of the mesial and distal carinae was also measured. The nomenclature used for the description of teeth is mesial (towards the snout), distal (away from this joint), lingual (towards the tongue), labial (towards the lip), apical (towards the tip of the tooth), and basal (towards the base of the tooth). For ornithischian teeth, maximum height is measured from the base of the crown to the tip of the apical cusp and the maximum mesiodistal length is measured between the flanks of mesial and distal most denticles. Isolated ornithischian teeth are difficult to assign to their original position in the jaw. Barrett (2001) has observed that tooth wear is predominantly present on the lingual cingula of maxillary teeth and labial cingula of dentary teeth. In the Kota teeth, no wear facets are observed with the exception of two specimens. However, distally offset apex is used as one criterion for orienting the specimens of both theropod and ornithischian teeth. Secondly, the convex face of the crown is interpreted as the labial side and the concave or flat face as the lingual side in both groups of dinosaurs. No attempt is made to assign the teeth to the maxillary or dentary bones as isolated teeth without wear facets are difficult to identify with these bones. In view of disarticulated nature of fossil material described, open nomenclature is followed for their systematic identification and description.



**Fig. 1.1** Location map and lithocolumn of the dinosaur teeth yielding section of the Kota Formation exposed at Paikasigudem village, Rebbana Mandalam, Adilabad district, Telangana, India

## Institutional Abbreviations

DUGF/J – Delhi University, Geology Department Fossil Collection/Jurassic), Delhi, India.

## Systematic Paleontology

Class Dinosauria Owen, 1842  
Order Ornithischia Seeley, 1887  
Ornithischia indet.

Morphotype 1

(Figs. 1.3A–H, 1.4A–S, 1.5A–H)

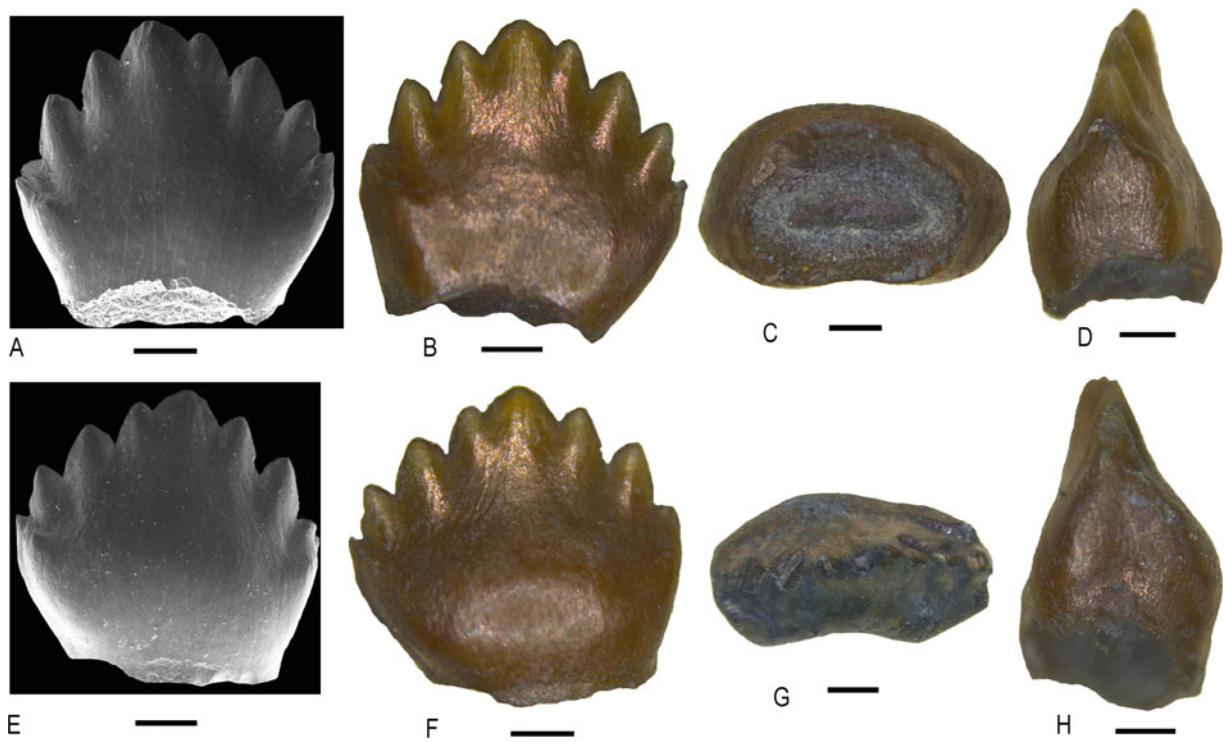
**Referred Material:** Five fairly well preserved cheek tooth (DUGF/J1-4, 12).

**Description:** DUGF/J1 is a well-preserved tooth lacking the root. It is as long mesiodistally as apicobasally high. The tooth is slightly asymmetrical in form, labiolingually compressed and appears broadly rounded in both labial and lingual views. The crown bears well-developed denticulated carinae mesially and distally. The occlusal tip of the crown has a relatively large and blunt cusp that is split into a smaller less individualized denticle on its mesial margin. The apex of the central cusp is slightly tilted distally. There are four major marginal denticles mesial to the apical cusp and three individualized denticles on its distal flank (Fig. 1.3A–B, E–F). Except for the mesial-most one, the denticles on the mesial carina are better developed than those situated distally. The denticles are bluntly rounded and conical or leaf-shaped in form. The median part of each denticle is strongly convex which makes its cross-section triangular in shape. The second mesial denticle from the apex is next to the apical cusp in size. In addition to the three regular denticles, a minute denticle is present at the base of the third





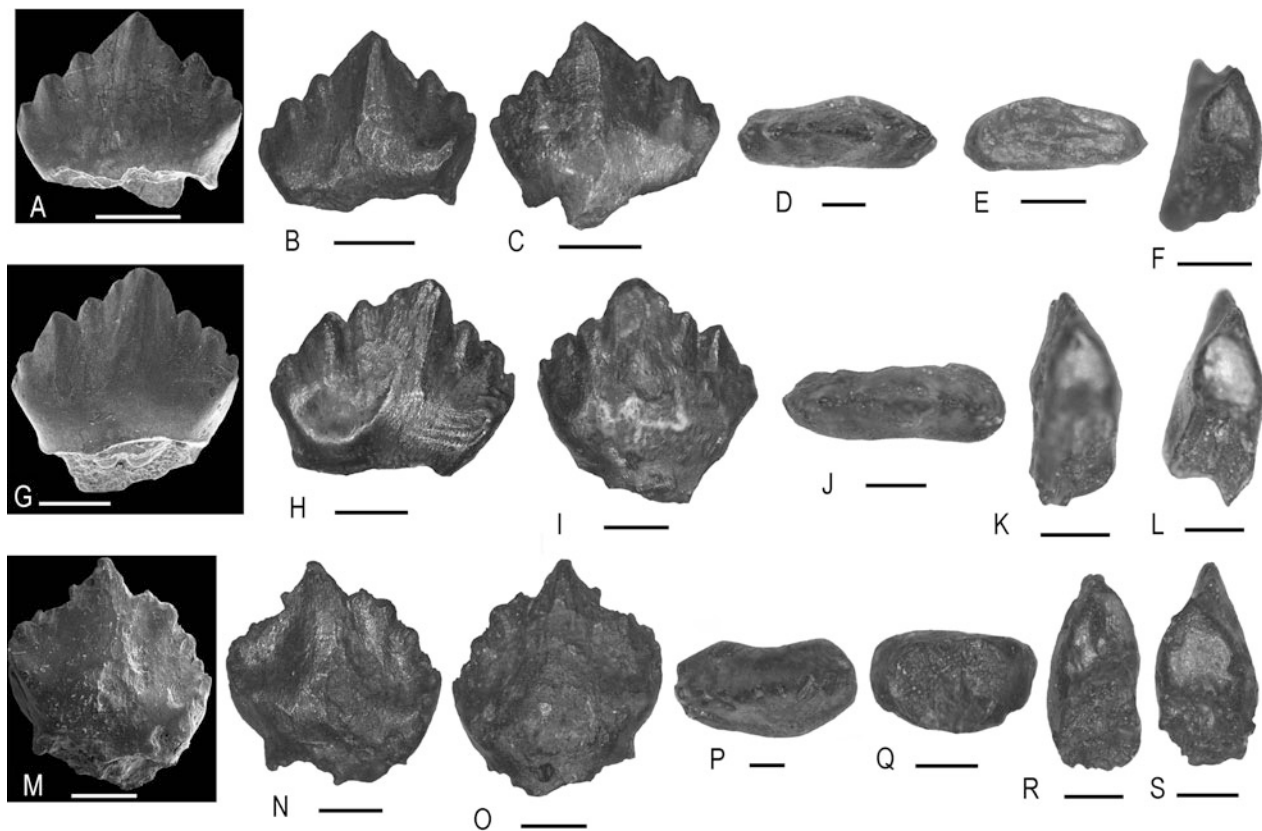
**Fig. 1.2** Field photograph of the fossiliferous section at Paikasigudem village, Rebbana Mandalam, Adilabad district, Telangana, India



**Fig. 1.3** Ornithischia indet. A–H. Morphotype 1, cheek tooth (DUGF/J1), A. lingual view (SEM photomicrograph), B. lingual view, C. basal view, D. view of mesial flank, E. labial view (SEM photomicrograph), F. labial view, G. occlusal view, H. view of distal flank. Scale bar equals 500  $\mu$ m

distal denticle, which is slightly lingually placed from the distal margin and terminates in a short rudimentary lingual ‘cingulum’. The marginal denticles though variable show a

general tendency towards decrease in size towards the base. The surface of the crown is covered by very faint striations that are more prominent labially. The labial crown surface is

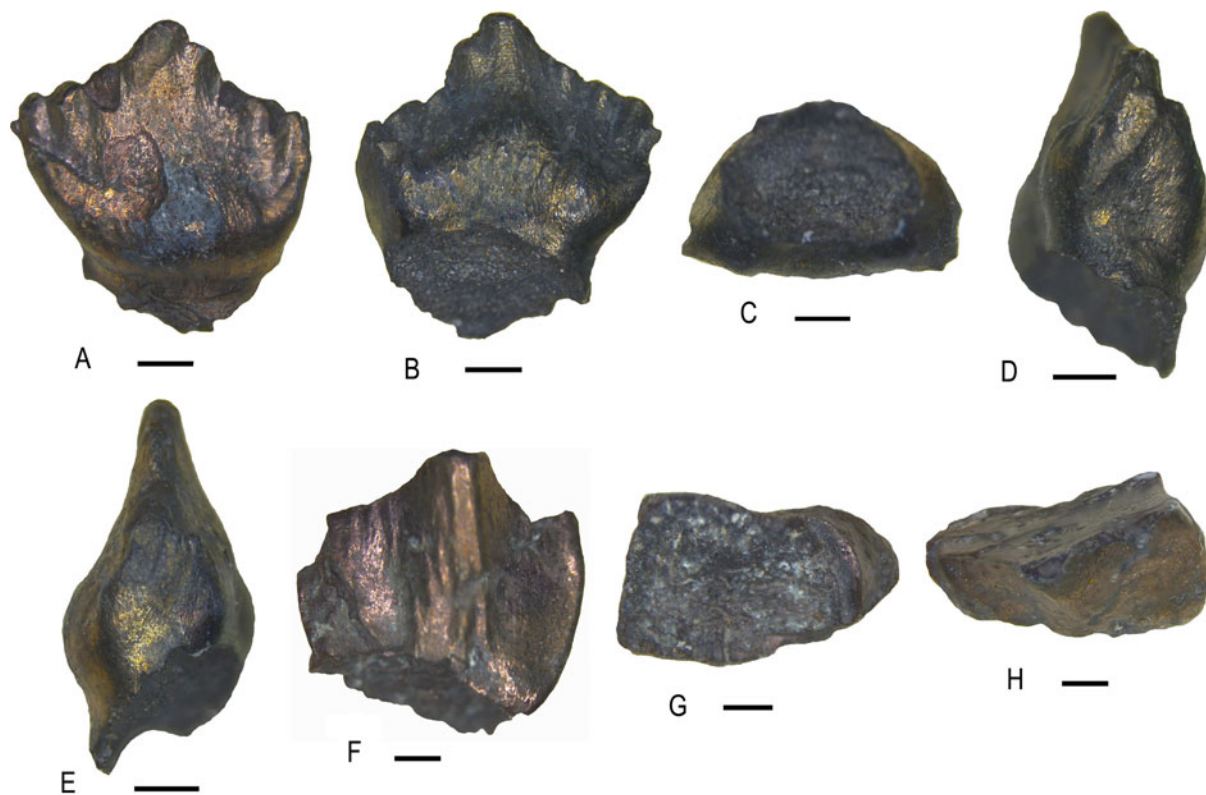


**Fig. 1.4** *Ornithischia* indet. **A–H.** Morphotype 1, cheek tooth (DUGF/J4), **A.** lingual view (SEM photomicrograph), **B.** lingual view, **C.** labial view, **D.** occlusal view, **E.** basal view, **F.** view of distal flank; **G–L.** Morphotype 1, cheek tooth (DUGF/J2), **G.** lingual view (SEM photomicrograph), **H.** lingual view, **I.** labial view, **J.** occlusal view, **K.** view of distal flank, **L.** view of mesial flank; **M–S.** Morphotype 1, cheek tooth (DUGF/J3), **M.** lingual view (SEM photomicrograph), **N.** lingual view, **O.** labial view, **P.** occlusal view, **Q.** basal view, **R.** view of distal flank, **S.** view of mesial flank. Scale bar equals 500  $\mu\text{m}$

strongly inflated at its base. As on the distolingual margin, a short rudimentary mesiolabial ‘cingulum’ is also present on the labial crown surface. The basal cross-section is bean-shaped with a concave lingual and convex labial margins (Fig. 1.3C). Flat distal and slightly concave mesial ‘interdental pressure facets’ are present. As there are resorption pits in the basal view of the crown, DUGF/J1 is considered as a shed tooth.

DUGF/J2–4 are relatively small in size (almost 50% smaller than DUGF/J1, Table 1.1) and have more asymmetrical crown with the apical cusp offset more distally than in DUGF/J1 (Fig. 1.4A–S). They are more labiolingually compressed, asymmetrically triangular in outline, as high as long and have an elliptical or lenticular basal cross-section. The apical cusp is broadly triangular in shape and relatively larger than the marginal denticles unlike in DUGF/J1 and has a convex lingual surface with a broad central ridge extending from the apex to the base of the crown. The crown is slightly concave at the lingual base of this ridge as in DUGF/J1. In DUGF/J2 (Fig. 1.4G–I), there are three denticles on the distal carina, of which the distal-most one is the

smallest whereas the remaining two are nearly of the same size. On the mesial carina, the first one from the apical cusp is very small and twinned with the latter, the second mesial denticle is slightly larger in size, the third one being the largest of all the mesial denticles, the fourth one is much smaller in size and is flanked by a miniscule denticle at the mesial extremity. The ‘interdental pressure facet’ is flat distally and concave mesially (Fig. 1.4K–L). The crown is convex labially and slightly concave lingually. The base of the crown, although swollen, is not as inflated as in DUGF/J1. The crown is laterally compressed rendering a lenticular outline to basal cross-section. The enamel surface displays very faint striations. In DUGF/J 3 (Fig. 1.4M–S), the apex of the tooth, particularly the carinae are broken but in general, the morphology is similar to that of DUGF/J2. DUGF/J4 (Fig. 1.4A–F), as compared to DUGF/J3, is mesiodistally longer than high and labiolingually compressed. The apical cusp is triangular in shape and relatively large and mesiodistally broader than in DUGF/J2 and 3. Both carinae bear three denticles each. The base of the crown in DUGF/J 4 is less swollen than in DUGF/J2 and 3.



**Fig. 1.5** Ornithischia indet. **A–E.** Morphotype 1, cheek tooth (DUGF/J12), **A.** labial view, **B.** lingual view, **C.** basal view, **D.** view of mesial flank, **E.** view of distal flank; **F–H.** Morphotype 2, cheek tooth (DUGF/J17), **F.** labial view, **G.** basal view, **H.** occlusal view. Scale bar equals 500  $\mu\text{m}$

The crown of DUGF/J12 is subtriangular to subtrapezoidal in shape with a large apical cusp and worn but relatively coarse marginal denticles (Fig. 1.5A–E). The marginal denticles extend some distance as cylindrical ridges separated by long grooves onto the body of the crown, particularly on the lingual crown face. There are four marginal denticles on either side of the apical cusp (Fig. 1.5A–B). The

first distal marginal denticle is smaller with respect to the apical cusp and is more or less at the same level as the latter and twins with it. Distal to this, three subequal denticles are present. At its distal extremity the distal carina curves lingually and extends to a short distance along the crown base before terminating in a minute denticle. The mesial carina bears three subequal denticles followed by a minute denticle

**Table 1.1** Measurements of ornithischian teeth

Specimen No.	Apicobasal height of the crown in mm	Mesiodistal length in mm
DUGF/J1	3.0	3.0
DUGF/J2	1.0	2.0
DUGF/J3	2.0	2.0
DUGF/J4	1.0	1.0
DUGF/J5	2.0	2.0
DUGF/J6	2.0	3.0
DUGF/J7	2.0	3.0
DUGF/J8	1.0	2.0
DUGF/J9	1.0	2.0
DUGF/J10	1.0	2.0
DUGF/J11	2.0	3.0
DUGF/J12	2.0	3.0
DUGF/J16	3.0 (in lingual view)	2.0 (in lingual view)
	2.0 (in labial view)	2.0 (in labial view)
DUGF/J17	3.0	3.0



at its mesial extremity. The lingual face of the crown is slightly concave (Fig. 1.5B), whereas the labial face is slightly convex (Fig. 1.5A), particularly in the middle part. The crown is swollen at its base to form a ‘cingulum’ which is more prominent on the lingual side. The lingual face of the crown is less high than the labial face and as a consequence the lingual swelling of the crown at its base is at a higher level than that of the labial face. On the lingual face of the crown, the swollen base is medially arched and connects to the apical cusp by a broad central eminence. Faint vertical grooves and ridges are present on this central eminence and on the basal swelling of the crown on this face (Fig. 1.5B). On the labial face, the crown is flanked by two narrow and obliquely oriented, elongated ridges that connect to the mesial and distal most denticles (Fig. 1.5A). The base of the crown is swollen both labially and lingually forming a distinct ‘cingulum’. The ‘interdental pressure facet’ is broad and flat distally, while it is broader than its distal counterpart and slightly concave mesially. At the labial base of the crown, a small part of the root is preserved which is narrower than the crown and is constricted from it. The basal cross-section is bean-shaped with a slightly indented lingual margin and a convex labial margin (Fig. 1.5C). All of the denticles exhibit wear facets at their apices. The wear facet on the mesial denticle next to the apical cusp extends down to its labial base. Another very broad and comma-shaped wear facet with its narrow and long axis paralleling the basal ‘cingulum’ occurs on the mesial half of the labial crown surface. Fine striae oriented parallel to the long axis of the crown are present on this wear facet.

**Remarks** Several characters of the maxillary/dentary teeth, such as low, sub-triangular shape in labial view, crowns mesiodistally expanded above the root such that the maximum mesiodistal length is greater than the maximum mesiodistal length of the root, labiolingual expansion of the crowns above the root forming a “cingulum”, asymmetrical crowns in mesial and distal views, and crowns with enlarged denticles on the mesial and distal margins often associated with ‘interdental pressure facet’ were considered as synapomorphies of Ornithischia (Serenó 1986, 1991; Hunt and Lucas 1994; Heckert 2002, 2004; Norman et al. 2004). However, recent reviews on Late Triassic dinosaurs have shown that some of these features are also present in non-dinosaurian Triassic archosaurs (Dzik 2003; Parkar et al. 2005; Butler et al. 2006; Irmis et al. 2007). Barrett et al. (2008) were of the opinion that the majority of these features are not known in non-ornithischian Jurassic archosaurs. However, the labiolingual expansion of the crown at its base or presence of a basal “cingulum” connected to the mesial and distal most denticles by ridges has been considered as an unambiguous synapomorphy for Ornithischia (Parkar et al. 2005; Butler et al. 2006; Irmis et al. 2007). Because of the

presence of asymmetric basal swelling of the crown in all the teeth described here, they are identified here as belonging to ornithischian dinosaurs.

In some symplesiomorphic characters such as labiolingually compressed, sub-triangular to triangular crowns with many denticles on mesial and distal carinae, smooth crown surfaces, these teeth compare well with those of basal ornithischian *Lesothosaurus diagnosticus* Galton (1978), basal thyreophorans *Scelidosaurus harrisonii* Owen (1861), *Scutellosaurus lawleri* Colbert (1981), *Emausaurus ernsti* Haubold (1990), *Laquintasaura venezuelae* Barrett et al. (2014) and the basal neornithischians *Agilisaurus louderbacki* Peng (1990) and *Hexinlusaurus multidens* (He and Cai 1984). However some of these taxa (*Scelidosaurus*, *Agilisaurus*) have tall, triangular to rhombic crowns which are apicobasally high in comparison to mesiodistally long and sub-triangular crowns of Kota teeth. In *Scelidosaurus*, the number of denticles on each margin vary from six to nine in comparison to three to four in the Kota teeth. *Emausaurus* differs from the Kota teeth in having slightly spatulate crowns. The maxillary and dentary teeth of *Scutellosaurus* and *Lesothosaurus* are identical to each other in sub-equal dimensions of mesiodistal length and apicobasal height, sub-triangular crown outlines, and bulbous crown base. But they differ from each other in the number of denticles on mesial and distal carinae. The Kota teeth although subtriangular in outline, their mesiodistal length is equal or greater than apicobasal height, the crown base is not as bulbous as in *Lesothosaurus* and *Scutellosaurus*, and have three to four denticles on each crown margin as compared six to nine denticles in *Lesothosaurus*. In contrast to subequal apicobasal height and mesiodistal length and smooth crowns of the Kota teeth, *Laquintasaura* and *Hexinlusaurus* have crowns that are apicobasally higher than mesiodistally long and apicobasal ridges on the crown surface. The maxillary/dentary teeth of heterodontosaurids also differ from the Kota teeth in having chisel-shaped crowns with denticles restricted to the apical most third of the crown (Butler et al. 2006). Although maxillary/dentary teeth of stegosaurs have sub-triangular crowns as in Kota teeth and some basal ornithischians, the “cingulum” is strongly developed and in the form of a horizontal ring around the crown base, the denticles are usually rounded at their tips as compared to sharply pointed denticles in other ornithischians, and vertical grooves extend from the apex of the denticles down to the ‘cingulum’ at the base (Blows and Honeysett 2014). The Kota teeth are also distinct from the teeth of iguanodontian and ceratopsid ornithischians in having sub-triangular crowns in labial/lingual view, coarse denticles on mesial and distal margins and asymmetry of the crowns in mesial and distal views (Serenó 1999; Butler et al. 2008).

In characters that are common to many ornithischian taxa such as leaf-like crown, labiolingual compression, twinned



apical cusp with adjacent mesial denticle, and asymmetrical basal swelling of the crown, the Kota teeth are broadly similar to those of an indeterminate ornithischian from the Middle Jurassic (Bathonian) of France (Kriwet et al. 1997), neornithischian *Nanosaurus agilis* Marsh (1877) known from the Upper Jurassic Morrison Formation (Carpenter and Galton 2018) and *Alocodon kuehnei* and *Phyllodon henkeli* from the Upper Jurassic Guimarota lignite deposits of Portugal (Thulborn 1973; Rauhut 2001), and the upper Bathonian Forest Marble Formation of southern England (Evans and Milner 1994). The Middle Jurassic teeth of France differ from those of Kota in the presence of well-developed secondary ridges connecting the denticles to the swollen base. In the cheek teeth of *Nanosaurus*, each denticle of posterior cheek teeth is divided into a central cusplet and adjacent blades reinforced with ridges that render a pointed triangular shape to its apex (Carpenter and Galton 2018, fig. 10H), whereas mid-dentary teeth have no such multi-cusped denticles (Carpenter and Galton 2018: fig. 10P). Moreover, in the Kota teeth, the ridges supporting the marginal denticles and associated grooves do not extend farther on to the crown as in *Nanosaurus*. The teeth of *Phyllodon* differ from DUGF/J1-4 and 12 in their lozenge shape, having apicobasal height greater than the mesiodistal length, and the labial side of the crown significantly higher than the lingual side. Similarly, *A. kuehnei*, referred variously to Fabrosauridae, Hypsilophodontidae, Ornithischia *incertae sedis* or Thyreophora (Thulborn 1973; Sereno 1991; Ruiz-Omeñaca 2001; Knoll 2002) or *nomen dubium* (Knoll 2002; Weishampel et al. 2004; Godefroit and Knoll 2003), differs from the Kota teeth in the presence of ridges on the lingual surface of the cheek teeth.

DUGF/J2-4 differ from DUGF/J1 in their smaller size, less swollen crown base, greater labiolingual compression, lenticular basal cross-section and a relatively broad and triangular apical cusp. Besides the size disparity, the morphological differences are sufficient enough to consider DUGF/J2-4 as representing different morphotype from that of DUGF/J1. These differences in morphology may be attributed either to their position on a different bone (dentary vs maxillary) or a different part of the tooth row (posterior vs anterior). DUGF/J4, previously described from the Kota Formation exposed at Gorlapalli village in Adilabad district, Telangana and situated about 40 km southeast of Paikasingudem site, was erroneously referred to Hypsilophodontidae (Prasad 1986).

DUGF/J12 is morphologically distinct from DUGF/J1-4 in having deep grooves separating cylindrical ridges of the denticles that extend some distance onto the crown and better expressed asymmetrical basal swelling of the crown or ‘cingulum’ which is arched below the apical cusp lingually. In size also it is intermediate to DUGF/J1 and DUGF/J2-4. The presence of a well-developed wear facet on the labial

‘cingulum’ indicates that DUGF/J 12 is a possible dentary tooth. Although its phylliform, labiolingually compressed and mesiodistally expanded crown with bulbous base, and well-developed constriction between the crown and root recall the crown morphology of ankylosaurian ornithischians, because of the poor preservation of DUGF/J12 and lack of synapomorphies of ankylosaurians, it is assigned to Ornithischia indet. Although there are significant morphological differences between these three sets of teeth, due to lack of knowledge on variation in dental morphology related to heterodonty, ontogeny, and intraspecific variation (Coombs 1990), they are lumped together in Ornithischia indet. Morphotype 1.

## Morphotype 2

(Fig. 1.5F–H)

**Referred Material:** One partially preserved tooth (DUGF/J17).

**Description:** DUGF/J17 is a partially complete crown. It is lozenge or sub-rhombic in shape with a high and large apical cusp flanked by two marginal denticles at the mesial and distal ends of the crown. The apex of the prominent apical cusp is slightly tilted distally. On one side of the crown, the apical cusp is connected to the base of the crown by a broad central eminence that extends from the apex to the base. The mesial and distal denticles are relatively small with respect to the apical cusp but salient and are connected to the crown base by narrow and low longitudinal ridges. The base of the crown is partly broken but from the preserved mesial part it appears to have a slightly swollen basal rim rather than a distinct ‘cingulum’. The mesial carina is convexly curved while the distal one is straight or less curved. There are no denticles on the mesial and distal carinae. The enamel of the lateral ridge connecting the distal denticle with the crown base is chipped off. Between these lateral ridges and the central eminence, the crown is longitudinally depressed. Five faint ridges are present distal to the central eminence (Fig. 1.5F). A smooth and flat vertical surface is present on the other side of the crown. This surface displays some fine striations oriented obliquely to the long axis of the crown. The mesial face of the tooth bears an acutely-triangular, concave ‘interdental pressure facet’. This facet is flat and relatively narrow on the distal flank. The basal cross-section is sub-trapezoidal in outline. In occlusal view, the crown presents a sub-rectangular outline with a broader mesial end than the distal one.

**Remarks** DUGF/J17 is a poorly preserved tooth but displays a steeply inclined wear facet with fine striae on one

side of the crown and one prominent subcentral vertical ridge and two marginal crests that descend basally to merge with the basal crown rim on the opposite side. Teeth with a prominent central ridge and two lateral ridges merging with basal crown rim are known to occur in heterodontosaurids such as *Echinodon*, basal thyreophorans and neornithischian *Agilisaurus*, which have triangular to rhomboidal crowns with denticulated margins (Galton 1986). DUGF/J17 differs from the basal ornithischian *Scelidosaurus* in lacking several small marginal denticles on the mesial and distal crown margins and in the presence of a prominent central ridge and fine longitudinal flutings on the crown surface. Contrary to the presence of a prominent central ridge in DUGF/J17, in *Echinodon*, there are no ridges on lingual or labial crown surfaces except for a rounded central eminence and the mesial and distal margins bear denticles. *Agilisaurus* also bears several marginal denticles both mesially and distally contrary to the condition of one denticle each at the mesial and distal flanks of the crown in DUGF/J17. The crown morphology of DUGF/J17 is somewhat similar to that of *Heterodontosaurus* in which the crown bears curved ridges running down the mesial and distal margins and meeting at the base forming a rim and enclosing a shield area. A central ridge as in DUGF/J17 divides the shield area of *Heterodontosaurus* teeth into two longitudinal depressions. However, in *Heterodontosaurus*, the occlusal surface displays characteristic 'w' shape wear facet and the crown merges into the root without forming a 'cingulum' (Norman et al. 2011). The root is not preserved and crown is heavily worn in DUGF/J17 making its identification difficult. In the absence of diagnostic crown features allying it with any known basal ornithischians, the present tooth is assigned to Ornithischia indet.

### Morphotype 3

(Fig. 1.6A–Q)

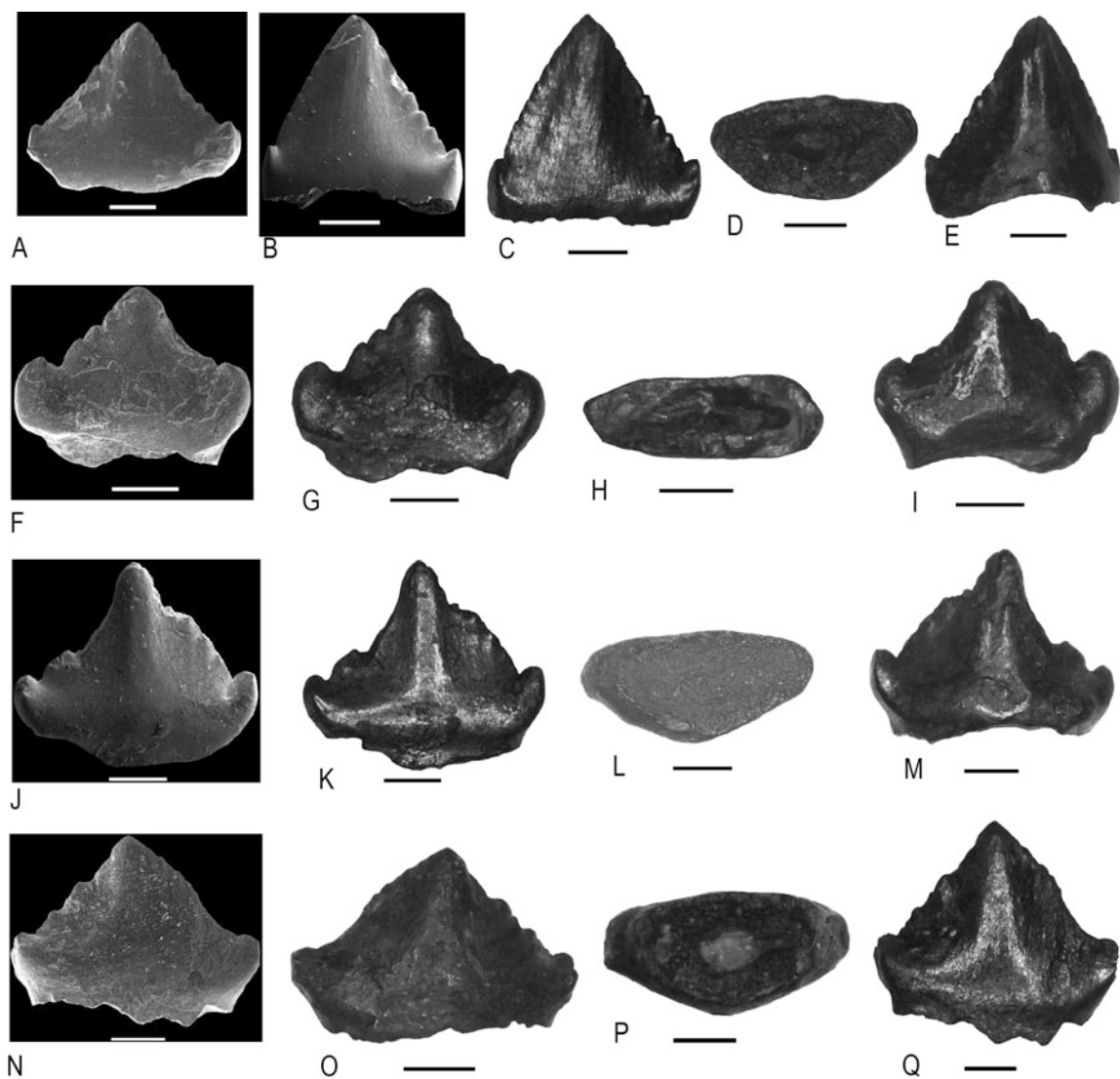
**Referred Material:** Seven fairly well-preserved teeth (DUGF/J5-11) and three fragmentary teeth.

**Description:** DUGF/J5-11 appear to belong to the cheek region. Only the crown is preserved in all the recovered teeth. DUGF/J5 (Fig. 1.6B–E) is higher than long and asymmetrical triangle in outline with a distally offset apex. The distal carina of the tooth is nearly straight while its mesial carina is slightly arched. The apical cusp is relatively broad in comparison to the marginal denticles and in the lingual view it extends basally in a broad and convex central eminence. On either side of the central eminence, the crown is flat on the lingual face. The mesial and distal carinae are finely denticulated with the denticles being smaller on the mesial carina than on the distal one. There are 7–8 denticles

on each carina. The mesial-most and distal-most denticles are salient and diverging away from the crown and form a short and faint 'cingulum' at the mesial and distal extremities. Except for these two denticles, the remaining denticles are minute and less conspicuous. The labial face of the crown is strongly convex. The surface of the crown is largely smooth. The crown is swollen at its base near its junction with the root. The basal cross-section of the crown presents an oval outline with a convex labial margin and nearly straight lingual border.

DUGF/J6-10 (Fig. 1.6A, F–Q) are more or less similar to DUGF/J5 in general crown morphology except for the fact that their mesiodistal length is nearly equal to their apicobasal height or slightly longer than high and they are not as asymmetrical as DUGF/J5. These teeth possibly represent middle cheek region. However, it is difficult to differentiate the maxillary and dentary teeth. In some of the teeth (DUGF/J5, 6 and 7), the crown shows faint vertical striations. The marginal denticles are not well preserved in all teeth, but in one tooth (DUGF/J7), there are at least seven denticles (Fig. 1.6A). In this tooth, the mesial carina is slightly longer than the distal one and is straight whereas the distal one is slightly concave. In all other morphological features, these teeth are similar to DUGF/J5. In all these teeth, the mesial and distal carinae intersect at right angles and the denticles decrease in size apically.

**Remarks** Although DUGF/J5 and DUGF/J6-10 differ in overall shape of the crown, salient and strongly diverging mesial most and distal most denticles and marginal denticles decreasing in size towards the apex are the characters that unite them in a single taxon. This variation in crown morphology may be due to variation in their position on the jaw. Thulborn (1973) described triangular, labiolingually compressed teeth that are as long as high and with apex canted distally, smooth enamel surfaces, straight lateral edges intersecting at right angles, marginal denticles decreasing in size towards the apex, and salient distal most and mesial most denticles diverging away from the crown from the Upper Jurassic lignite deposits of Guimarota at Porto Pinheiro, near Lourinhã, Provincia do Estremadura, Portugal. These teeth were assigned to a new ornithischian taxon *Trimucrodon cuneatus* within the Hypsilophodontidae. Thulborn (1973) suggested that *Alocodon kuehnei* and *T. cuneatus* were closely related to *Fabrosaurus australis* and might be referred to the Fabrosauridae. Later, Galton (1994) described additional teeth of *Trimucrodon* from the Upper Jurassic Guimarota lignite deposits. Morphologically, the Kota teeth are indistinguishable from those of Guimarota. Thulborn (1973) opined that *Trimucrodon cuneatus* is closely related to *Echinodon becklesii* Owen (1861), a heterodontosaurid (Norman and Barrett 2002) known from the Middle Purbeck Beds, Durlston Bay, U.K. in many of



**Fig. 1.6** Ornithischia indet. A–S. Morphotype 3. **A.** cheek tooth (DUGF/J7), labial view (SEM photomicrograph); **B–E.** ?mesial cheek tooth (DUGF/J5), **B.** lingual view (SEM photomicrograph), **C.** lingual view, **D.** basal view, **E.** labial view; **F–I.** cheek tooth (DUGF/J9), **F.** lingual view (SEM photomicrograph), **G.** lingual view, **H.** basal view, **I.** labial view; **J–M.** cheek tooth (DUGF/J8), **J.** lingual view (SEM photomicrograph), **K.** lingual view, **L.** basal view, **M.** labial view; **N–Q.** cheek tooth (DUGF/J6), **N.** lingual view (SEM photomicrograph), **O.** labial view, **P.** basal view, **Q.** lingual view. Scale bar equals 500 μm

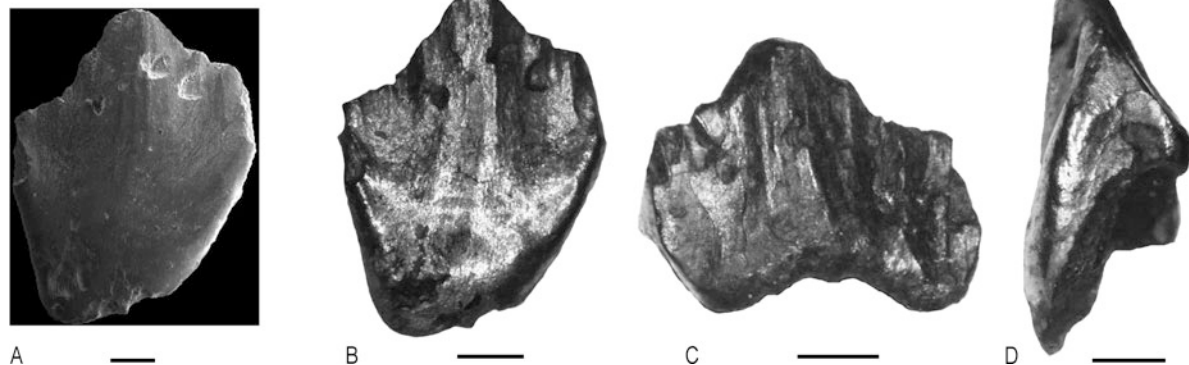
the above cited morphological features. However, *Trimucrodon* teeth differ from those of *Echinodon* in having fewer marginal denticles that disappear well below the apex of the crown and more strongly divergent mesial most and distal most denticles. Galton (1978) also felt that there are more differences than similarities between *Echinodon* and *Trimucrodon*. Though Weishampel and Witmer (1990) considered both *T. cuneatus* and *A. kuehnei* as *nomina dubia*, Sereno (1991) placed them in *Ornithischia incertae sedis*. In light of these taxonomic uncertainties, the teeth from the Kota Formation are referred here to *Ornithischia* indet.

#### Morphotype 4

(Fig. 1.7A–D)

**Referred Material:** One fairly well-preserved tooth (DUGF/J16).

**Description:** In DUGF/J16, the crown is asymmetrical, laterally compressed, and lozenge-shaped with a high central cusp with its tip slightly tilted distally. In the lingual view, the crown is slightly concave or flat and slightly higher than mesiodistally long. On both labial and lingual surfaces, the middle of the crown is enlarged into a broad central



**Fig. 1.7** Ornithischia indet. A–D. Morphotype 4, cheek tooth (DUGF/J16), A. lingual view (SEM photomicrograph), B. lingual view, C. labial; view, D. view of distal flank. Scale bar equals 500  $\mu\text{m}$

eminence. There are two narrow lateral ridges that flank the crown mesially and distally. Broad longitudinal depressions separate these ridges and the central eminence. The mesial denticulated margin is relatively longer than the distal one and both these carinae are slightly concave. Two small denticles separated by narrow longitudinal grooves are present on the mesial carina, whereas there are three such minute denticles on the distal carina. The base of the crown is produced into a slightly swollen rim. The crown is broader near the apical region than at its base which is tapering down gradually. The crown surface shows faint striations on the lingual crown surface (Fig. 1.7A–B) but these are more salient on the labial face (Fig. 1.7C). The labial crown surface is slightly convex, less high than the lingual one and the basal enamel rim is located at the level of mid lingual crown height. This could be an artifact of breakage. It has a slightly arched, swollen base. The crown is laterally compressed and has a basal sub-elliptical to sub-quadrangular cross-section. The tips of the marginal cusps are slightly worn labially. Wear facets are also observed on the mesial and distal flanks of the crown labially. The mesial and distal flanks of the crown base are slightly concave and flat, respectively.

**Remarks** The basal thyreophoran *Laquintasaura* and basal neornithischian *Huxinlusaurus* have apicobasally high crowns as in DUGF/J16, the crown is triangular in shape in *Laquintasaura* and the crown surface is ornamented with well-developed apicobasal ridges in both *Laquintasaura* and *Huxinlusaurus*. The crown morphology of DUGF/J16 is more close to that of heterodontosaurids. Heterodontosaurids are primarily known by *Lycorhinus angustidens* Haughton (1924), *Abriktosaurus consors* (Thulborn 1974), *Heterodontosaurus tucki* Crompton and Charig (1962), *Pegomastax africanus* Sereno (2012) from the Lower Jurassic (Hettangian–?Sinemurian) Upper Elliot Formation, South Africa, *Manidens condorensis* a small-bodied heterodontosaurid from the Middle Jurassic Cañadón

Asfalto Formation in central Patagonia, Argentina (Pol et al. 2011), *Tianyulong confuciusi* from the latest Middle Jurassic (Callovian) upper horizon of the Lanqi (= Tiaojishan) Formation in Liaoning Province, northern China (Zheng et al. 2009) and *Fruitadens haagarorum* from the Upper Jurassic (Tithonian) Morrison Formation (Butler et al. 2010, 2012). DUGF/J16 compares well with the cheek teeth of heterodontosaurids, particularly with *L. angustidens* and *A. consors* in being slightly higher than long, spatulate in form, apex slightly deflected distally, crown expanding in mesiodistal length towards the apex, two to three denticles occurring towards the apex of the crown, the middle part of the crown both labially and lingually forming a broad central eminence, and less robust mesial and distal ridges converging at the base forming a swollen rim or weak ‘cingulum’. In *Heterodontosaurus*, there is no basal rim, rather the crown merges with the root. Further, in *Heterodontosaurus* and possibly in *Lycorhinus* as well, the broad central eminence is in the form of a strong ridge in contrast to its weak development in DUGF/J16 and *Abriktosaurus*. DUGF/J16 displays longitudinal enamel ridges on the labial crown surface, but the labial crown face is less high than its lingual counterpart possibly due to breakage in this region. DUGF/J16 is also somewhat similar to the teeth described as *Iguanodontia* gen. et sp. indet. from the Upper Jurassic strata of Guimarota lignite mine, Portugal (Rauhut 2001: fig. 5A–B) in the crown shape, development of central eminence and lateral ridges and absence of prominent secondary ridges. Because of absence of secondary ridges, the specimens from Portugal were not assigned definitively to *Iguanodon*. DUGF/J16 is also comparable to dentary/maxillary teeth described under *Ceratopsia* indet. from the Lower Cretaceous Shale and Fuxin formations, northeastern China (Amiot et al. 2010: fig. 7, V16748.10) on account of laterally compressed, lozenge-shaped crown with a central primary ridge and the mesial and distal secondary ridges forming a rim at the base and the lingual crown higher than



its labial counterpart. However, in the Chinese specimens, the labial crown face seems to be smooth as compared to ridged labial crown face with an arched swollen base in DUGF/J16. All known heterodontosaurid taxa share one synapomorphy i.e., dentary and maxillary cheek teeth are chisel-shaped with denticles restricted to the apical most third of the crown (Weishampel and Witmer 1990; Norman and Barrett 2002; Galton 2002; Norman et al. 2004). The presence of ‘cingulum’ or basal swelling of the crown was considered as a valid synapomorphy used for the identification of ornithischians (Parkar et al. 2005; Butler et al. 2006). However, ‘cingulum’ is absent or weakly developed in several ornithischian taxa, such as *Heterodontosaurus tucki* and *Abrictosaurus consors* (Heterodontosauridae), and an unusual heterodontosaurid from the Late Triassic of Argentina (cf. *Heterodontosaurus* sp., Baez and Marsicano 2001) and derived members of the clade Ornithopoda (Butler et al. 2006). In most other heterodontosaurids, the ‘cingulum’ is weakly developed (Hopson 1980; Norman and Barrett 2002). Though the Kota specimen appears to be similar to maxillary/dentary teeth of heterodontosaurids in general shape (chisel-shape) and weak development of ‘cingulum’, because of poor preservation it is regarded as an indeterminate ornithischian.

#### Morphotype 5

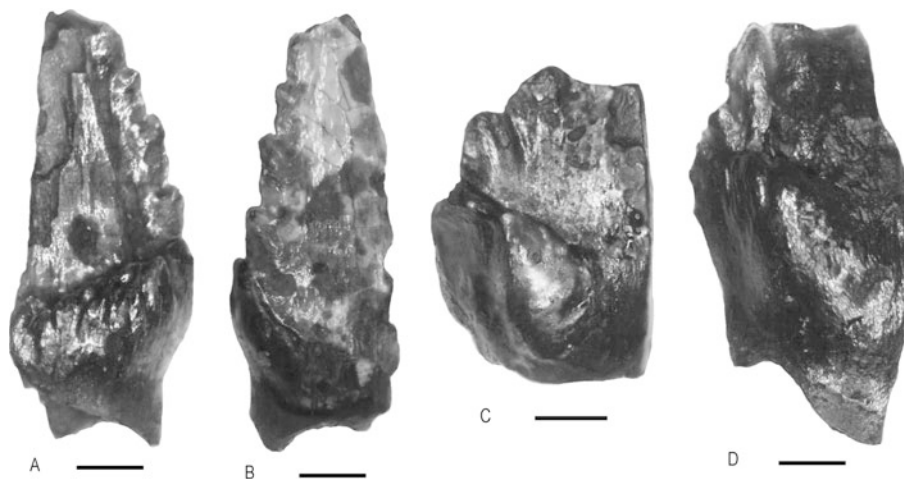
(Fig. 1.8A–D)

**Referred Material:** Three fragmentary teeth (DUGF/J13–15).

**Description:** There are three fragmentary teeth (DUGF/J13–15, Fig. 1.8A–D) with only a small longitudinal

part preserved. A couple of marginal denticles are preserved in DUGF/J13–14 (Fig. 1.8C, D). The vertical grooves between adjacent marginal denticles do not extend far onto the crown flank. A distinct cingular ridge extends from the mesial or distal most denticle towards the middle of the crown on the inferred lingual face. In one specimen (DUGF/J 14), the ‘cingulum’ is finely crenulated (Fig. 1.8 D). In DUGF/15 (Fig. 1.8A, B), the crown is more elongated apicobasally than in other specimens (possibly leaf-like), and the ‘cingulum’ is thick extending onto the middle part and the crown surface is longitudinally grooved. However, the marginal denticles are small and not separated by deep grooves as in DUGF/J13–14.

**Remarks** The two fragmentary teeth DUGF/J13–14 have similar development of ‘cingulum’, coarse marginal denticles and the grooves between them. The fragmentary nature of these teeth do not permit any taxonomic assignment beyond Ornithischia indet. DUGF/J15 is closer to ankylosaurid teeth on account of elongated crown (leaf-like) and the widely spaced marginal denticles with shallow grooves between them. DUGF/J15 with a more elongated (higher than long) crown and marginal denticles not separated by deep grooves and a ‘cingulum’ extending on to the middle part resembles the teeth described under *Gargoyleosaurus* and *Ankylosaurus* by Blows and Honeysett (2014: figs. 4D, 5B) from the Early Cretaceous of England. In possessing apicobasally extending ridges on its enamel, DUGF/J15 equally compares with the crown morphology of maxillary or dentary teeth described as *Laquintasaura* from the Lower or Middle Jurassic La Quinta Formation of western Venezuela (Barrett et al. 2008: fig. 4) and *Hexinlusaurus* from the Middle Jurassic of China (He and Cai 1984; Barrett et al. 2005). However, in *Hexinlusaurus*, the crown has a rhombic outline compared to the triangular outline of *Laquintasaura*



**Fig. 1.8** Ornithischia indet. Morphotype 5, **A–B.** cheek tooth fragment (DUGF/J15), **A.** lingual view; **B.** labial view; **C.** cheek tooth fragment (DUGF/J13), ?lingual view; **D.** cheek tooth fragment (DUGF/J14), ?lingual view; Scale bar equals 500  $\mu$ m

and the inferred triangular outline of DUGF/J15. Though DUGF/J15 exhibits dental characters similar to those of the basal ornithischian *Laquintasaura*, in view of limited fossil material at hand, the fragmentary tooth from the Kota Formation is conservatively referred to an indeterminate ornithischian.

Order Saurischia Seeley, 1887

Suborder Theropoda Marsh, 1881

Family Dromaeosauridae Matthew and Brown, 1922

Dromaeosauridae indet.

(Fig. 1.9A–AE)

**Referred Material:** Twenty six fairly well preserved (DUGF/J19-38, 43-48) and six fragmentary teeth.

**Description:** Based on morphological differences, the teeth are described below under five different morphotypes.

#### Morphotype 1

DUGF/J19-25 (Fig. 1.9A–R) have relatively broad-based crowns, slightly recurved with a nearly straight distal margin and convex mesial margin. In all these teeth, the root is not preserved. The labial face of the crown is strongly convex, while the lingual face is flat to slightly convex in the middle. A convex and broad central eminence extends from the base towards the apex where it becomes narrow (DUGF/J19). In some of these teeth (DUGF/J19, 21, 22-24), the middle part of the convex lingual face is flat (DUGF/J23-25). The tip of these teeth is slightly lingually canted. The mesial and distal carinae bear denticles, but the distal denticles are comparatively larger than the mesial ones. On both carinae, the denticles are larger in the middle and decrease in size apically and basally. The denticles on the distal carina are oriented perpendicular to the longitudinal axis at the base of the crown but towards the apex their tips get slightly apically curved. Denticles are almost as high as they are long. In DUGF/J22, the mesial carina does not bear any denticles. This face shows a tear-drop shaped wear tapering down the mesial carina from the apex. A small wear facet also occurs just below the apex on the distal carina. The surface is smooth but appears to have very fine longitudinal striations. DUGF/J25 has a moderately deep attritional furrow that extends from the apex to one-third height of the crown on its lingual face and an oval basal cross-section. This tooth is less compressed labiolingually than the other teeth. In DUGF/J19-21, the mesial carina terminates one-third height above the crown base and is slightly lingually twisted. In DUGF/J22-23 and 25, though it terminates before reaching the base, the mesial carina occupies midline of the mesial

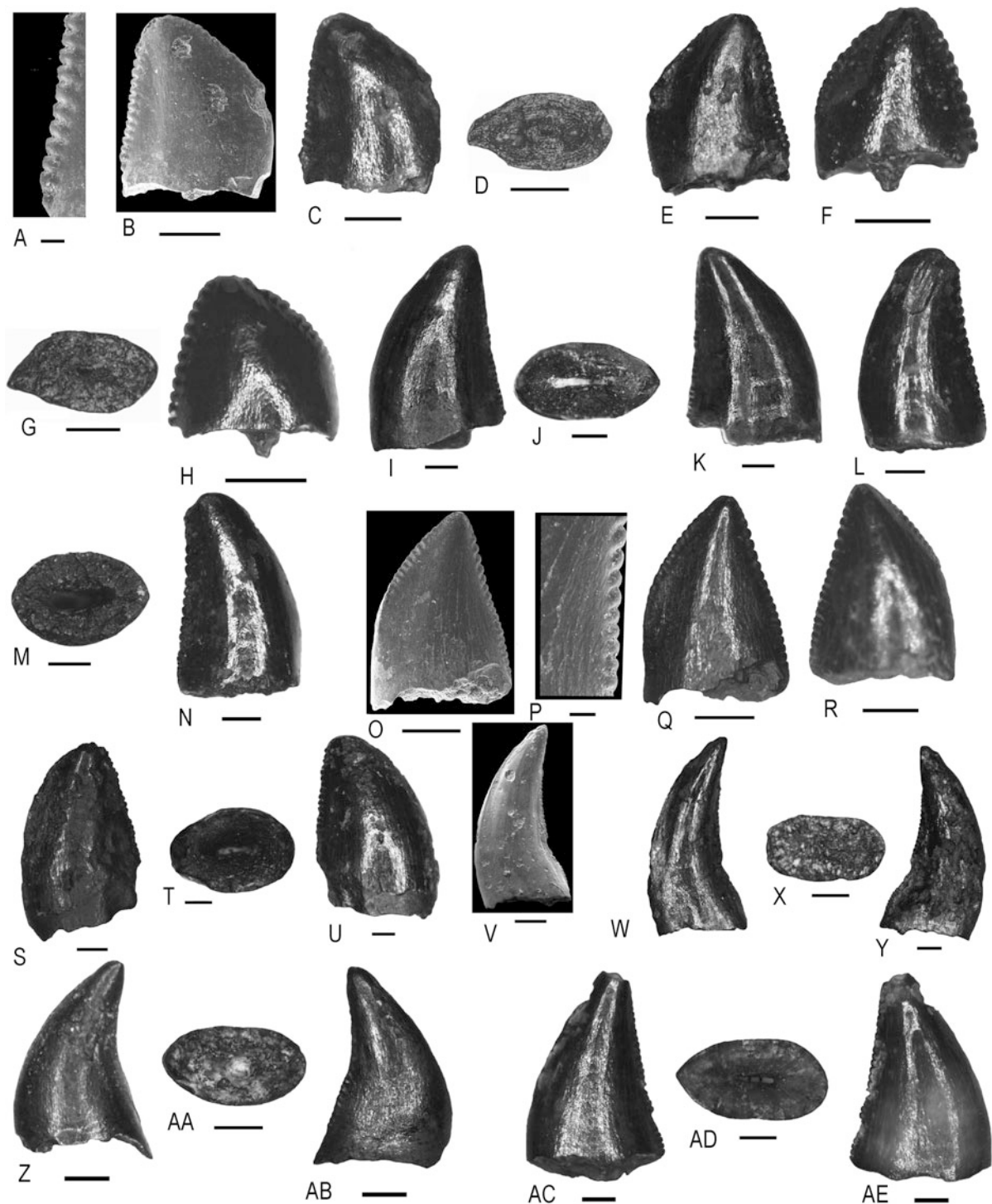
margin. The basal cross-section is tear-drop shaped in DUGF/J19, 21, 22, 24, 25 and elliptical to oval in DUGF/J20 and 23. A longitudinal groove which tapers towards the apex is present on the central eminence of the lingual face of most of these teeth.

#### Morphotype 2

DUGF/J27-30, 32-34 (Fig. 1.9V-AB) are more strongly distally recurved than those of Morphotypes 1 and 3 with a strongly convex mesial carina and concave or straight distal carina. The tip of the crown extends slightly beyond the base distally in DUGF/J28, whereas it does not extend beyond distal base in rest of the teeth referred to this morphotype. In one of the better preserved larger specimens (DUGF/J29), the mesial carina twists lingually about one-fourth the distance from the apex and terminates before reaching the base. The mesial carina is not denticulated in these teeth. The distal margin is concave and the carina bears relatively larger denticles in the middle and the denticles decrease in size apically and basally. The distal carina, occupying a middle position along the distal margin, terminates at the base of the tooth and its denticles are perpendicular to the long axis at the base and have slightly apically tilted tips towards the apex. The mesial margin of the crown is rounded as compared to labiolingually compressed distal margin. On the lingual face, a broad convex eminence extends from the apex to the base of the crown medially, but at the base it becomes flattened with a central shallow groove. The labial surface is convex in the middle and mesially but a shallow longitudinal depression exists between the central broad ridge and the distal margin. The crown base is elliptical in outline in DUGF/J29 whereas DUGF/J27, 28, 30 and 33 have oval cross-sections.

#### Morphotype 3

DUGF/J26 (Fig. 1.9S–U) is comparatively larger in size than the teeth referred to Morphotype 1 (Table 1.2). In this tooth, the lingual face of the tooth is less flattened than in Morphotype 1, rather the median part is convex and in the form of a broad eminence with laterally depressed areas near the carinae. The mesial carina is convex and the distal one is rectilinear as in Morphotype 1. The apex is slightly lingually canted and blunt. It is also tilted distally. The distal carina, which is broken at its base, bears small, chisel-shaped denticles which are perpendicular to the long axis of the crown. On the mesial margin of the crown, the enamel is heavily etched and probably had minute denticles. The mesial carina is better preserved in the apical half of the crown and appears to have been slightly twisted lingually. The labial face of the crown is uniformly convex with a slight longitudinal depression between the distal carina and the broad median



**Fig. 1.9** A–AE. Isolated teeth of *Doromaosauridae* indet. A–R. Morphotype 1, A–E (DUGF/J21), A. enlarged view of distal carina (SEM photomicrograph), B. labial view (SEM photomicrograph), C. labial view, D. basal view, E. lingual view; F–H (DUGF/J20), F. lingual view, G. basal view, H. labial view; I–K (DUGF/J22), I. labial view, J. basal view, K. lingual view; L–N (DUGF/J25), L. lingual view, M. basal view, N. labial view; O–R. (DUGF/J19), O. lingual view (SEM photomicrograph), P. enlarged view of distal carina (SEM photomicrograph), Q. lingual view, R. labial view; S–U. Morphotype 3 (DUGF/J26), S. lingual view, T. basal view, U. labial view; V–AB. Morphotype 2, V–Y (DUGF/J29), V. lingual view (SEM photomicrograph), W. lingual view, X. basal view, Y. labial view; Z–AB (DUGF/J32), Z. lingual view, AA. Basal view, AB. labial view; AC–AE. Morphotype 4 (DUGF/J36), AC. lingual view, AD. basal view, AE. labial view. Scale bar equals 500  $\mu$ m for B–O, Q–AE and 100  $\mu$ m for A and P

**Table 1.2** Measurements of theropod teeth

Specimen no.	TCH	FABL	BW	CBR (TCH/BW)	MDC	DDC	DSDI
DUGF/J19	2.00	1.00	0.70	1.42	16/1mm	13/1.0 mm	1.23
DUGF/J20	1.00	1.00	0.60	1.66	15/1.0 mm	13/1.0 mm	1.15
DUGF/J21	2.00	1.00	0.70	1.42	Poorly preserved	13/1.0 mm	
DUGF/J22	3.00	2.00	1.00	2.00	No denticles	11/1.0 mm	
DUGF/J23	2.00	1.00	0.90	1.11	16/1.0 mm	14/1.0 mm	1.14
DUGF/J25	3.00	2.00	1.00	2.00	Worn	7.5/1.0 mm	
DUGF/J26	4.00	2.00	2.00	1.00	Heavily worn	11/1.0 mm	
DUGF/J27	3.00	1.00	0.70	1.42	No denticles	11/1.0 mm	
DUGF/J28	2.00	1.00	0.60	1.66	No denticles	7.5/1.0 mm	
DUGF/J29	3.00	2.00	0.90	2.22		13.5/1.0 mm	
DUGF/J30	2.00	1.00	0.80	1.25	No denticles	No denticles	
DUGF/J31	2.00	1.00	0.80	1.25	No denticles	Weakly developed	
DUGF/J32	2.00	2.00	0.80	2.50	No denticles	11/1.0 mm	
DUGF/J33	3.00	1.00	0.80	1.25	No denticles	Not preserved	
DUGF/J34	2.00 tip broken	1.00	0.70	1.42	No denticles	14/1.0 mm	
DUGF/J35	1.00	0.70	0.50	1.40		20/1.0 mm	
DUGF/J36	3.00	2.00	1.00	2.00	No denticles	10.5/1 mm	
DUGF/J37	2.00	1.00	0.80	1.25	9.0/1.0 mm	8.0/1.0 mm	1.25
DUGF/J39	4.00	2.00	1.00	2.00		14/1.0 mm	
DUGF/J45	2.00	2.00	1.00	2.00	14/1.0 mm	11/1.0 mm	1.27
DUGF/J46	3.00	3.00	1.00	3.00	No denticles	10/1.0 mm	
DUGF/J52	2.00	1.00	0.80	1.25	No denticles	12/1.0 mm	
DUGF/J53	3.00	1.00	0.90	1.11	No denticles	16/1.0 mm	
DUGF/J54	2.00	1.00	0.70	1.42		16/1.0 mm	
DUGF/J55	3.00	0.80	0.70	1.14		15/1 mm	
DUGF/J56	3.00	1.00	1.00	1.00	No denticles, only flange	12.5/1 mm	
DUGF/J60	2.00	1.00	1.00	1.00	No denticles	13/1mm	
DUGF/J61	4.00	1.00	0.90	1.11	18/1.0 mm	12/1.0 mm	1.50
DUGF/J62	3.00	1.00	1.00	1.00	No denticles	13.5/1.0 mm	
DUGF/J63					No denticles	18/1.0 mm	
DUGF/J64	3.00	0.90	0.70	1.28	22/1.0 mm	18/1.0 mm	1.22
DUGF/J65	3.00	0.90	0.70	1.28	19/1.0 mm	14/1.0 mm	1.35
DUGF/J68	Apex broken	1.0	1.0	1.0	16/1.0 mm	12/1.0 mm	1.33

BW = basal width, CBR = crown base ratio, DSDI = denticle size difference index, FABL = fore-aft basal length, MDC = mesial carina denticle count per mm, DDC = distal carina denticle count per mm, TCH = tooth crown height

longitudinal eminence. The basal cross-section is oval in form with a slight indentation at the distal margin of the lingual face. DUGF/J26 is less labiolingually compressed than the teeth of Morphotypes 1 and 2.

#### Morphotype 4

DUGF/J36 (Fig. 1.9AC–AE) has a broad base, triangular outline, denticulated distal and non-denticulated mesial margin, flat labial and lingual surfaces in the middle of the crown, chisel-like denticles perpendicular to the long axis of the crown at the base and inclined towards the apex in the apical region, and lenticular cross-section. The longitudinal groove present on the central eminence of the lingual face of teeth belonging to morphotype 1 and 2 is not distinct on this tooth.

#### Morphotype 5

DUGF/J43–48 (Fig. 1.10A–Q) are incompletely preserved teeth characterized by triangular crowns and strong labiolingual compression. DUGF/J43, broken at its base, is a better preserved specimen of the six referred teeth (Fig. 1.10A–E). This tooth is recurved distally with a convex mesial margin and slightly concave distal margin and its apex is slightly canted lingually. The mesial and distal carinae are denticulated and the distal denticles are larger than the mesial ones. On both carinae, the denticle tips are pointing towards the apex. In DUGF/J43 and 44, however, the denticles of the distal carina are perpendicular to the long axis at the base. The lingual face of the crown in DUGF/J43 is in the form of a convex broad eminence in the middle which slopes laterally towards the mesial and distal carinae



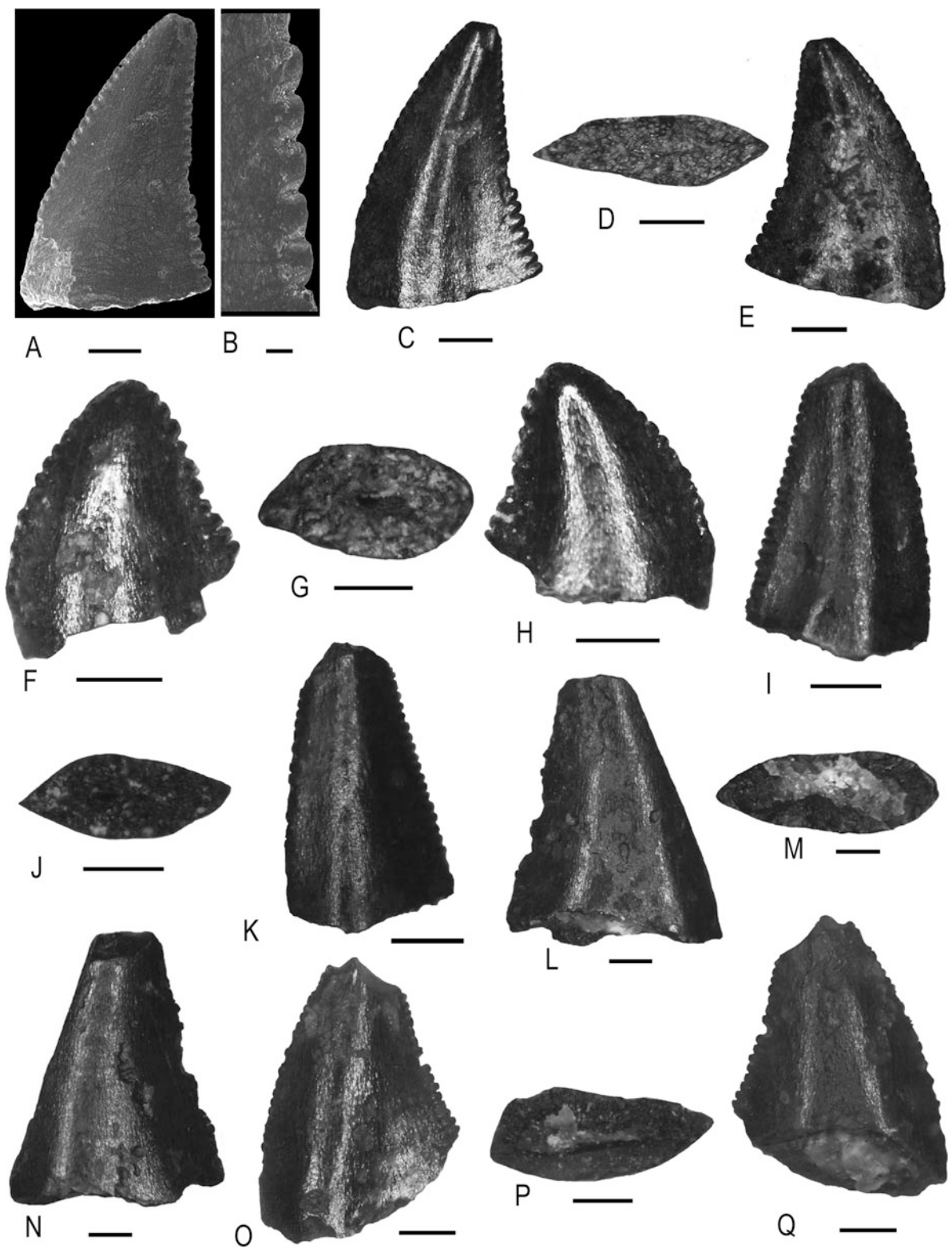
(Fig. 1.10C). Whereas in DUGF/J 44, the lingual face of the crown is covered by a broad, flat to slightly convex longitudinal eminence that extends from the apex to the base (Fig. 1.10I). This median eminence is separated from the mesial and distal carinae by shallow and narrow longitudinal depressions. On the labial surface of all teeth, a medial convex eminence extends from the apex to the base which gently slopes to the mesial margin. This central eminence is separated from the distal carina by a shallow longitudinal groove and the distal margin is more expanded laterally in the basal half forming a labiolingually compressed flange. Along this flange the denticles become comparatively larger than in the apical half. Because of the labiolingual compression, the teeth have a lenticular cross-section. DUGF/J37-38 also display a crown morphology very similar to that of DUGF/J43-48, but DUGF/J37 has a tear drop-shaped basal cross-section (Fig. 1.10G) in comparison to oval or lenticular cross-section of DUGF/J43-48 (Fig. 1.10D, J, M, P).

**Remarks** Isolated theropod dinosaur teeth are difficult to distinguish at genus and species level as many of their morphological features, such as crown basal length and width, crown height, presence or absence of denticles on mesial and distal carinae, denticle shape, density and orientation on the carina, are similar in many theropod dinosaur groups (Hendrickx and Mateus 2014; Gerke and Wings 2016). Besides this, differences in dental morphology due to position in the jaw, intraspecific and ontogenetic variations are poorly understood at present. However, many recent works have adapted morphometric methods to assign isolated teeth at least to higher taxonomic levels (Smith et al. 2005; Fanti and Therrien 2007; Larson 2008; Larson and Currie 2013; Hendrickx and Mateus 2014; Gerke and Wings 2016). Because of limited number of theropod teeth recovered from the Kota Formation, only qualitative morphological features are used in the present study for identifying them at higher taxonomic levels.

The labiolingual compression and recurvature of the Kota teeth with mesial and distal serrations are plesiomorphic characters observed in theropod dinosaurs. In view of their diminutive size, the taxonomic affinity of the Kota teeth with Tyrannosauroidae, Allosauroidae, Carcharodontosauridae, Ceratosauridae and Megalosauridae is ruled out. The small-sized Kota teeth may have come from juvenile individuals or small-sized theropod taxa. Han et al. (2011) while describing similar-sized theropod teeth from the Middle-Upper Jurassic Shishugou Formation, China discussed their possible derivation from juveniles or adults of dromaeosaurids (Osborn 1924; Xu et al. 2000; Norell et al. 2006), compsognathids (Currie and Chen 2001), troodontids (Sankey et al. 2002), basal ornithomimosaurs (Perez-Moreno et al. 1994), and primitive alvarezsauroids (Choiniere et al.

2010). Lateral teeth of Compsognathidae differ from those of the Kota Formation in lacking mesial denticles, distal denticles disappearing well beneath the apex of the crown and in the presence of a constriction between the crown and root (Currie and Chen 2001; Peyer 2006; Dal Sasso and Maganuco 2011; Hendrickx and Mateus 2014). Among troodontids, *Troodon* differs from all the Kota morphotypes in its less recurved teeth with large, apically inclined distal denticles and constriction between the crown and the root (Currie et al. 1990), whereas *Byronosaurus* (Makovicky et al. 2003), *Mei* (Xu and Norell 2004), *Urbacodon* (Averianov and Sues 2007) and *Anchiornis* (Hu et al. 2009) are distinct from the Kota teeth in having non-serrated margins and a constriction between crown and root. In the presence of unserrated and basally constricted teeth, basal ornithomimosaurs such as *Pelicanimimus* (Perez-Moreno et al. 1994) and *Shenzhousaurus* (Ji et al. 2003) are distinctly different from the Kota teeth. Basal alvarezsauroids are also distinguished from the Kota teeth in having several vertical ridges on the labial surface of the crown (Han et al. 2011).

Dromaeosaurid teeth are relatively small in size, moderately labiolingually compressed and strongly curved distally, and bear mesial and distal carinae with prominent denticles at least on the distal carina and have a sigmoidal carina in mesial view with some lingual twisting (Currie et al. 1990; Sankey et al. 2002). Lingual spiraling or twisting of mesial carina is also known in basal tyrannosauroid *Guanlong* (Han et al. 2011), some tyrannosaurids (Sankey et al. 2002) and allosauroids (Currie and Carpenter 2000). In *Dromaeosaurus* and basal tyrannosauroid *Guanlong*, the lingual twisting of the mesial carina begins almost at the apex (Han et al. 2011), whereas in Kota Morphotypes 1–3, the mesial carina descends a short distance from the apex before twisting lingually as in isolated dromaeosaurid teeth from Barremian of Uña, Spain (Rauhut 2002). The relatively small and moderately laterally compressed teeth described here under Morphotypes 1–3 exhibit distally curved crowns with a twisted mesial carina, oval cross-section (with a rounded mesial margin and a more acute distal margin), fore-aft basal length twice basal width, lack of constriction between the crown and root, denticles either on both carinae or restricted to the distal one, when both carinae are denticulated, distal ones slightly larger than the mesial ones, and chisel-shaped distal denticles placed perpendicular to the long axis of the carina at the base and slightly tilted apically near the tip that conform to the dental morphology described for Dromaeosauridae (Currie et al. 1990; Basso 1997; Han et al. 2011; Sankey et al. 2002; Hendrickx and Mateus 2014; Gerke and Wings 2016). The tooth described under Morphotype 4 differs from those of Morphotypes 1–3 in lacking the lingual twist of mesial carina and in having less labiolingually compressed crowns. Rather they have straight mesial carina. Teeth similar to those of *Dromaeosaurus* with



**Fig. 1.10** A–Q. Isolated teeth of *Dromaeosauridae* indet., Morphotype 5. A–E (DUJF/J43), A. lingual view (SEM photomicrograph), B. enlarged view of distal carina at its base (SEM photomicrograph), C. lingual view, D. basal view, E. labial view; F–H (DUGF/J37), F. labial, G. basal, H. lingual; I–K (DUGF/J44), I. lingual, J. basal, K. labial; L–N (DUGF/J46), L. lingual, M. basal, N. labial; O–Q (DUGF/J45), O. labial, P. basal, Q. lingual. Scale bar equals 500 µm for A, C–Q and 100 µm for B

a straight mesial carina were reported earlier also (Currie et al. 1990). Keeping this in view, Morphotype 4 is tentatively referred to Dromaeosauridae indet. until more taxonomically diagnostic specimens are found. Dromaeosaurids teeth are known to exhibit considerable variation in shape, some being long and fang-like or resembling curved daggers, some being short and strongly hooked (Longrich 2008), while others have a figure of eight in cross-section caused by concavities on labial and lingual surfaces of the crown (e.g. *Buitreraptor* [Makovicky et al. 2005; Gianechini et al. 2011], *Austroraptor* [Novas et al. 2009]). The denticles are also variably present or absent in premaxillary, maxillary and dentary teeth and on mesial and distal carinae in *Microraptor*, *Tsaagan*, *Bambiraptor*, *Shanag* (Xu et al. 2000; Hwang et al. 2002; Burnham 2004; Hwang 2005; Norell et al. 2006) and *Sinornithosaurus* (Xu and Wu 2001). Lateral teeth of dromaeosaurids *Buitreraptor*, *Dromaeosaurus* and *Saurornitholestes* are characterized by a crown morphology distinct from other dromaeosaurids. *Buitreraptor* lacks denticles on both mesial and distal carinae (Gianechini et al. 2011). In *Dromaeosaurus*, the carinae bear sub-quadrangular denticles with convex margins (Currie et al. 1990; Currie 1995), whereas in *Saurornitholestes*, the teeth bear large and apically hooked denticles. In light of these observed variations in dental morphology of Dromaeosauridae, though the teeth referred to Morphotype 5 approach the crown morphology of velociraptorine dromaeosaurids (Currie et al. 1990) in their strong lateral compression, distal curvature of crown apex, location of mesial carina on the midline of the crown, shape of the denticles and the size difference observed between the denticles of mesial and distal carinae (DSDI 1.25–1.27), it is conservatively included in Dromaeosauridae.

Prior to this report, Jurassic dromaeosaurid teeth have been documented from the Middle Jurassic (Bathonian) Isalo Group (Isalo IIIb) of the Mahajanga Basin, northern Madagascar (Maganuco et al. 2005), the Middle Jurassic (Bathonian) of the UK (Evans and Milner 1994), the Middle–Upper Jurassic Shishugou Formation of northwest Xinjiang, China (Han et al. 2011), the Upper Jurassic Guimarota lignite deposits of Portugal (Zinke 1998), the Upper Jurassic of Germany (van der Lubbe et al. 2009; Gerke and Wings 2016), and the Upper Jurassic – Lower Cretaceous succession of Galve area, NE Spain (Sanchez-Hernandez et al. 2007). The teeth belonging to Morphotypes 1–5 of the Kota Formation fall within the size range of those from UK, Guimarota (Portugal), Shishugou (China) and Galve (Spain). The DSDI measured for a few of the Kota teeth with denticles on both carinae falls within the range of 1.15–1.23. This value is slightly higher than 0.86–1.17 and 1.0 measured for dromaeosaurid teeth from the Lower Cretaceous of Uña, Spain (Rauhut 2002) and the Upper Jurassic of Portugal (Zinke 1998), respectively, but is within the range of

1.2 measured for dromaeosaurid teeth from the Late Jurassic – Early Cretaceous of Galve, Spain (Sanchez-Hernandez et al. 2007).

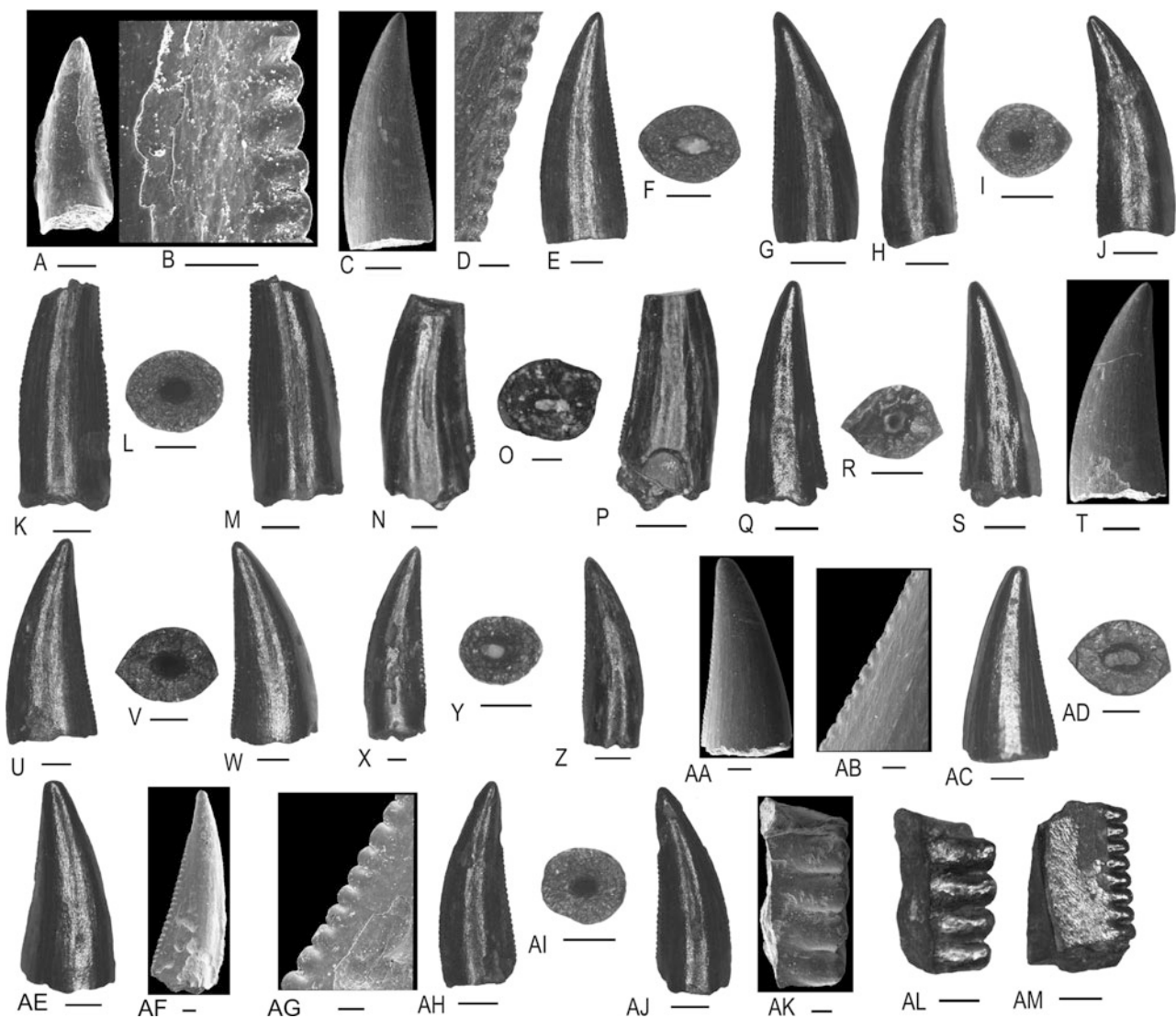
#### *Richardoestesia*-like teeth

(Fig. 1.11A–AJ)

**Referred Material:** 22 fairly well-preserved (DUGF/J39, 49–69) and four fragmentary teeth (DUGF/J70–73).

**Description:** The teeth are moderately labiolingually compressed, lanceolate or triangular with apicobasally elongated crowns and have suboval basal cross-section. The tip of the crown is slightly distally recurved and lingually canted. The mesial margin of the tooth is convexly rounded, whereas the distal margin is nearly straight. The lingual face of the teeth is moderately convex in the middle and in the form of a broad eminence extending from the apex to the base. The labial face of the crown is more convex than the lingual face. A shallow, medial longitudinal groove is present on both labial and lingual faces of the crown which gradually disappears towards the apex. Some of these teeth are slightly constricted at the crown-root junction due to rounding of the tooth at the base of mesial and distal carinae (Fig. 1.11A, K–M, X–Z). A few teeth (DUGF/J56, 60, 61–63, and 71) have slightly broader bases (Fig. 1.11 T–W, AA, AC–AE) as compared to narrow bases of majority of the teeth. In one set of teeth, only the distal carina is denticulated (DUGF/J49–61) (Fig. 1.11C, E, G, Q, S, X, Z, AA–AC, AE), while the second set of teeth have mesial denticles as well which are relatively small in size as compared to the distal ones (DUGF/J62, 64–65, 68, 72) (Fig. 1.11H–J, K, M, AF–AI, AJ). These teeth have broad, mesiodistally short minute denticles with tips that are square-shaped or rounded and oriented perpendicular to the long axis. The denticles decrease in size towards the apex and also towards the base. Interdentine spaces are minute and less discernible. In one specimen (DUGF/J54; Fig. 1.11Q–S), the lingual face at one-third height of the base is constricted with two shallow and elongated depressions on either side of the median ridge. The relevance of this constriction is not known. Faint longitudinal (apicobasal) striations are present on both labial and lingual faces of the crown in some specimens (e.g., DUGF/J61). The basal cross-section of these teeth is oval or rounded oval.

DUGF/J39 (Fig. 1.11N–P) is an elongated tooth with a broken apex. This tooth is morphologically similar to those described above except for the presence of longitudinal flutings on its labial and lingual faces. The distal carina bears minute denticles oriented perpendicular to the long axis of the crown at its basal one-fourth, whereas rest of this carina is worn flat. The mesial carina is also worn flat, but shows traces of worn denticles and terminates before reaching the base at least



**Fig. 1.11** A–AJ. Isolated teeth of *Richardoestesia*-like teeth. A–B (DUGF/J50), A. lingual view (SEM photomicrograph), B. enlarged view of distal carina (SEM photomicrograph); C–G (DUGF/J61), C. lingual view (SEM photomicrograph), D. enlarged view of distal carina (SEM photomicrograph), E. lingual view, F. basal view, G. labial view; H–J (DUGF/J64), H. labial view, I. basal view, J. lingual view; K–M (DUGF/J68), K. lingual view, L. basal view, M. labial view; N–P (DUGF/J39), N. labial view, O. basal view, P. lingual view; Q–S (DUGF/J54), Q. lingual view, R. basal view, S. labial view; T–W. (DUGF/J56), T. lingual view (SEM photomicrograph), U. lingual view, V. basal view, W. labial view; X–Z (DUGF/J55), X. lingual view, Y. basal view, Z. labial view; AA–AE (DUGF/J62), AA. labial view (SEM photomicrograph), AB. enlarged view of distal carina (SEM photomicrograph), AC. lingual view, AD. basal view, AE. labial view; AF–AJ (DIUGF/J65), AF. labial view (SEM photomicrograph), AG. enlarged view of distal carina (SEM photomicrograph), AH. lingual view, AI. basal view, AJ. labial view; AK–AM. Theropoda indet. AK–AL (DUGF/J41), AK. in labial or lingual view (SEM photomicrograph), AL. in labial or lingual view; AM (DUGF/J40) in labial or lingual view. Scale bar equals 100  $\mu$ m for B, D, AB, AG, and AK, 300  $\mu$ m for A, and 500  $\mu$ m for E–AF, AH–AJ, AL, and AM

one-fourth the height of the crown from the base. The tip is broken perpendicular to the long axis and a wear facet extends slightly labially at its middle region. The basal cross-section is oval to elliptical in outline with a broadly rounded mesial margin and laterally compressed distal margin.

**Remarks** In having lanceolate shape and minute denticles as compared to the tooth size, these teeth are comparable to those of *Richardoestesia* described from the Upper

Cretaceous strata of North America (Currie et al. 1990; Basso 1997; Longrich 2008; Sankey 2008; Larson 2008; Larson et al. 2010; Larson and Currie 2013). *Richardoestesia* has a long stratigraphic range from Santonian to Maastrichtian and a wide geographic distribution in North America, extending from West Texas to southern Alberta (Larson and Currie 2013; Sankey 2001; Sankey et al. 2002, 2005; Larson 2008). At present, *Richardoestesia* is known by three named species, *R. gilmorei* from the Upper



Cretaceous (Campanian) Dinosaur Park Formation of southern Alberta (Currie et al. 1990), *R. isosceles* from the Upper Campanian Aguja Formation, Texas (Sankey 2001), and *R. asiatica* from the Upper Cretaceous (Turonian) Bissekty Formation, central Kyzylkum Desert, Uzbekistan (Sues and Averianov 2013). According to Sankey et al. (2002), the teeth of *R. gilmorei* are strongly recurved resembling those of *Sauromitholestes*, whereas the teeth of *R. isosceles* have a shape of isosceles triangle. Moreover, the denticles of *R. gilmorei* are pointed as compared to their squarish appearance in *R. isosceles*. The teeth of *R. asiatica* are characterized by straight mesial and distal margins, labiolingually flattened crown and the presence of triangular central depression at the base, both labially and lingually. Besides the occurrences from Canada, USA and Uzbekistan, *Richardoestesia*-like teeth have also been documented from the Upper Jurassic Guimarota coal mine, Portugal (Zinke 1998), the Lower Cretaceous localities at Uña (Rauhut and Zinke 1995) and Galve, Spain (Rauhut 2002), the Upper Cretaceous deposits of southcentral Pyrenees (Prieto-Márquez et al. 2000) and the Upper Cretaceous (Maastrichtian) Ocozocoautla Formation of Chiapas, southern Mexico (Carbot-Chanona and Rivera-Sylva 2011).

The teeth of *R. gilmorei* differ from the Kota specimens in the curvature of the proximal part and mesiodistally broad crown bases, pointed denticles and flattened oval to oval cross-section. In *R. isosceles*, the teeth are not constricted at the crown base and have a trapezoidal cross-section at the base (Sankey et al. 2002). Furthermore, the teeth of *R. gilmorei* and *R. isosceles* are characterised by subequal mesial and distal denticles as in the teeth from the Upper Jurassic Guimarota lignite mine (Zinke 1998) and the Lower Cretaceous of Uña (Rauhut and Zinke 1995). This is contrary to the smaller mesial denticles of the present teeth and the Upper Cretaceous teeth from Uzbekistan (Sues and Averianov 2013), Mexico (Carbot-Chanona and Rivera-Sylva 2011) and the San Juan Basin, northwestern New Mexico (Williamson and Brusatte 2014). The longitudinal groove, generally present on the labial and lingual faces of *R. gilmorei*, *R. isosceles* (Currie et al. 1990; Sankey et al. 2005), *R. asiatica* (Sues and Averianov 2013) and cf. *Richardoestesia* sp. from the Upper Jurassic of Guimarota (Zinke 1998) and the Lower Cretaceous of Galve (Rauhut 2002), are also present on many of the Kota teeth. *Richardoestesia*-like teeth from the Late Cretaceous of the south-central Pyrenees (Prieto-Márquez et al. 2000), Chiapas, southern Mexico (Carbot-Chanona and Rivera-Sylva 2011), and New Mexico (Williamson and Brusatte 2014) have denticles on the distal carina only as in some teeth from the Kota Formation. The Mexican teeth, however, differ from the Kota specimens in having mesiodistally expanded crowns with a less flattened oval cross-section. DUGF/J 39 with longitudinal flutings and minute denticles on the distal carina with respect to the size of

the tooth is comparable to *Richardoestesia* sp. described from the Upper Cretaceous Lance Formation, USA (Longrich 2008: fig. 9.8F). The basal constriction observed in the teeth of *R. gilmorei* and in the teeth from San Juan Basin, New Mexico (Williamson and Brusatte 2014), is also present in some of the Kota teeth (DUGF/J 55, 68). Though the denticles are chisel-shaped in the Guimarota, Uña and Kota teeth, the mesial denticles in the Kota teeth are smaller than the distal ones. The DSDI of the Kota teeth with denticles on both carinae is 1.22 for DUGF/J 64, 1.33 for DUGF/J 68, 1.35 for DUGF/J 65, and 1.50 for DUGF/J 61. The DSDI ranges between 1.08 and 1.5 for cf. *Richardoestesia* sp. from the Lower Cretaceous of Uña, Spain (Rauhut 2002) and from 0.80 to 1.33 for cf. *Richardoestesia* sp. from the Upper Jurassic of Portugal (Zinke 1998). Hence the DSDI of the Kota conforms to the values documented for *Richardoestesia* from Jurassic and Cretaceous sites.

The teeth from the Kota Formation of India, the Upper Jurassic of Portugal and Lower Cretaceous of Spain closely resemble the North American species *R. isosceles* in having elongated crowns with an isosceles triangular shape that might indicate a long temporal range for this clade. It may also be the result of convergent evolution as suggested by Zinke (1998). In the past, *Richardoestesia* has not been identified with any known families below the clade Maniraptora within the order Theropoda as its phylogenetic relationships were not clear (Currie et al. 1990). Some considered *Richardoestesia* as a possible spinosaurid or as a product of convergent evolution with spinosaurids (Sankey et al. 2002), whereas others regarded them as troodontids (Hwang 2005). On re-examining *R. gilmorei*, Longrich (2008) suggested that it may be referred to Paraves. A piscivorous diet was suggested for *Richardoestesia* because of the lanceolate shape of the teeth and high abundance in near coastal deposits such as Hell Creek and Lance formations (Basso 1997; Sankey 2001; Longrich 2008). However, based on cladistic and quantitative analyses of isolated theropod teeth from the Upper Jurassic of Portugal Hendrickx and Mateus (2014) identified a tooth (ML 939) as *Richardoestesia* aff. to *R. gilmorei* and placed *Richardoestesia* in the Dromaeosauridae. Following Hendrickx and Mateus (2014), *Richardoestesia*-like teeth from the Kota Formation are assigned to the Dromaeosauridae.

Theropoda indet.

(Fig. 1.11AK-AM)

**Referred Material:** Two tooth fragments (DUGF/J/40-41).

**Description:** There are two fragments (DUGF/J 40-41) representing one of the dental carinae in the Kota microvertebrate fossils. Of these, the denticles of DUGF/J40

(Fig. 1.11AM) are smaller than those of DUGF/J41 (Fig. 1.11AK–AL). The denticles are cylindrical, chisel-like in form with their mesiodistal length greater than their apicobasal height. The denticles are oriented perpendicular to the long axis of the carinae. The blood grooves are prominent and deeply developed extending up to the base of the denticles. However, they do not bend basally at their contact with the crown surface as in allosaurids or tyrannosaurids.

**Remarks** These specimens are too fragmentary to comment on their taxonomic affinity and are thus left in open nomenclature.

## Discussion

Prior to the present finds from the Kota Formation, a partial skull and postcranial skeleton, attributed to a stegosaur *Dravidosaurus blanfordi*, was described from the Coniacian Trichinopoly Group within the *Kosmaticeras theobaldianum* Zone exposed near Siranattam village, Cauvery Basin, South India (Yadagiri and Ayyasami 1979). However, its identification as a stegosaur was questioned by some (Chatterjee and Rudra 1996; Wilson et al. 2011), while others considered it as *nomen dubium* (Maidment et al. 2008) or ?Stegosauria indet (Pereda Suberbiola et al. 2015). It is the first record of an ornithischian dinosaur from India. Presence of an ornithischian tooth in the Kota Formation was noted by Prasad (1986) though it was wrongly identified as a hypsilophodontid. Following a detailed study of supposed ornithischian dinosaur bone identified as a stegosaur dermal plate from the Upper Cretaceous Kallamedu Formation (Anonymous 1978), Galton and Ayyasami (2017) concluded that this bone probably belongs to a sauropod. They, however, agreed with the referral by Mateus et al. (2011) of a right pes impression from the Upper Cretaceous (Maastriichtian) Lameta Formation of the Jetholi area, Balasinor, Kheda district, Gujarat, western India (Mohabey 1986) to stegosaurian ichnotaxon *Deltapodus* sp. Ankylosaur bones comprising spines, limbs and girdle elements are also known to occur in the Lameta Formation at Rahioli in Gujarat, western India (Chatterjee 2020). The presence of ornithischian remains in the Upper Triassic Upper Dharmaram Formation of the Pranhita-Godavari Valley was also mentioned by Kutty et al. (1987), but these fossils have not yet been described or illustrated.

In comparison to well documented early sauropod skeletons from the Kota Formation (*Barapasaurus tagorei* Jain et al. 1975; *Kotasaurus yamanapalliensis* Yadagiri et al. 1979), no theropod and ornithischian dinosaur remains have been reported so far except for one report of a supposed hypsilophodontid tooth (Prasad 1986) and alleged carnosaur

(Yadagiri 1982) and ankylosaur (Nath et al. 2002). Yadagiri (1982) reported the occurrence of fragmentary ischium, dorsal and caudal vertebrae and isolated tooth representing a supposed carnosaur in the Kota Formation under a new taxon *Dandakosaurus indicus* (Theropoda *incertae sedis*) in a progress report submitted to the Geological Survey of India. This remained inaccessible in the classified unpublished field reports of the Geological Survey of India. Neither a full description nor illustrations of this find have been published so far and thus regarded as *nomen nudum*. Purported ankylosaur bones consisting of parts of the skull, maxillae and dentaries, vertebrae, 30 specimens of body armor, fragments of ilium and scapula and teeth were reported from the red clays of the Kota Formation occurring below the limestone (Nath et al. 2002). However, the illustrated tooth (Nath et al. 2002: plate 1, fig. e) appears little like an ankylosaurid tooth, rather it compares well with a crocodilian tooth. The bones reported by Nath et al. (2002) were regarded as those of a crocodylomorph (Wilson and Mohabey 2006: 471). However, Galton and Carpenter (2016: 203) identified the dermal armor of Nath et al. (2002) as Thyreophora indet. The present study provides evidence for greater diversity in the dinosaur fauna of the Kota Formation, particularly for the small dinosaur fauna. The occurrence of a scute and fragmentary limb bone of possible scelidosaurid affinity in the Kota Formation has also been noted (Chatterjee 2020).

The Paikasigudem section of the Kota Formation has not yielded any large vertebrates so far and the vertebrate microfossils recovered range in size from 1 to 8 mm. Although the teeth described are limited in number and have relatively few diagnostic features, we can make reasonably acceptable taxonomic inferences on the presence of several ornithischian and theropod morphotypes. The dinosaur fauna described here is clearly represented by small individuals <10 kg body weight as is the case with the dinosaur fauna from the Upper Jurassic Guimarota Coal Mine (Rauhut 2001) and many other such microfaunas. The most commonly present teeth in the Kota assemblage are those of *Richardoestesia*. The predominance of theropod teeth in the assemblage is similar to the Guimarota fauna. Isolated teeth with resorption pits indicate that they are shed teeth. The microvertebrate assemblage from the Paikasigudem section is primarily represented by small-sized fauna as in the cases of Guimarota and Uña sites (Zinke 1998; Rauhut 2001, 2002), and most of the Middle Jurassic vertebrate microsites of UK (Evans and Milner 1994; Sweetman 2004). Apparently it could be an artifact of size sorting of the fauna before its burial. But there are no visible evidences for long distance transport in the vertebrate microfossils recovered from the studied section. Alternatively, the environmental niche may have favored small bodied taxa.

Although the fossil material described is fragmentary in nature, it improves our current understanding of vertebrate

diversity of the Kota Formation. It also adds to our knowledge on limited fossil data available for ornithischian and theropod dinosaurs of the Gondwana. The large number of morphotypes present in the ornithischian and theropod dinosaur teeth assemblage of the Kota Formation indicates that the taxonomic diversity is relatively high though identification at lower taxonomic levels is not possible because of the absence of taxon specific synapomorphies and poor preservation of some of the teeth. On a conservative note, we can conclude that there are at least five distinct taxonomic units of early ornithischians within the seven morphological variants of indeterminate ornithischians described. Similarly, there are at least a minimum of three distinct taxonomic units (one dromaeosaurid, one *Richardoestesia*-like, one indeterminate) among the seven theropod morphotypes. However, more well-preserved and unambiguously associated fossil material is needed to know the real diversity of Kota dinosaur fauna.

Some of the earliest records of dromaeosaurid dinosaurs came from the Middle Jurassic Isalo Group (Isalo IIIb) of Mahajanga Basin, Madagascar (Maganuco et al. 2005; Flynn et al. 2006), the Middle Jurassic (Bathonian) Chipping Norton Limestone Formation at Hornsleasow Quarry, Gloucestershire, England (Metcalf et al. 1992), the Middle Jurassic (Upper Bathonian) Forest Marble, Kirtlington Quarry, UK (Evans and Milner 1994), the Middle-Upper Jurassic Shishugou Formation, northwest Xinjiang, China (Han et al. 2011), the Middle Jurassic Balabansai Svita in the northern Fergana depression, Kyrgyzstan (Averianov et al. 2005), the Upper Jurassic (Tithonian) Mugher Mudstone Formation of Ethiopia (Goodwin et al. 1999; Hall and Goodwin 2011), the Upper Jurassic of Boulonnais, northern France (Buffetaut and Martin 1993), and the Upper Jurassic (Kimmeridgian) of Portugal (Zinke 1998; Hendrickx and Mateus 2014), and the Upper Jurassic of Germany (van der Lubbe et al. 2009; Gerke and Wings 2016). All these reports were based on tooth morphotypes. It is evident from this list that the geographic distribution of dromaeosaurid dinosaur is skewed towards the Laurasian continents and the apparent scarcity of coelurosaurian clades in the former Gondwana is an artifact of poor sampling in these localities.

The age of the Kota Formation has remained problematic as conflicting ages were suggested on the basis of different fossil groups. In general, the Early Jurassic age was favored based on weak biostratigraphic correlations of different vertebrate groups (Jain 1973, 1980, 1983; Yadagiri and Prasad 1977; Evans et al. 2001), whereas the Middle Jurassic age was suggested using ostracod and palynological data (Govindan 1975; Vijaya and Prasad 2001). As there are no marine intercalations within the Kota Formation, no biostratigraphic constraints are available from marine microfossils. Likewise, no radiometric dates are available for the Kota Formation as it contains no volcanic ash beds or

associated radiometrically datable horizons. The new fossils described here provide some constraints on the age of this formation. Until now, some of the oldest records of *Phylodon* and *Alocodon*-like (*Ornithischia incertae sedis*) teeth came from the Lower-Middle Bathonian Chipping Norton Limestone Formation (Metcalf et al. 1992; Metcalf and Walker 1994), Upper Bathonian Stonesfield Slate (Galton 1980) and Kirtlington (Evans and Milner 1994). The oldest dromaeosaurids are known from the Middle Jurassic (Bathonian) of UK (Evans and Milner 1994). The Kota sauropod dinosaurs *Barapasaurus* and *Kotasaurus* are of similar evolutionary grade as *Cetiosaurus* of UK. As the ornithischian and dromaeosaurid taxa as well as other vertebrate groups from the Middle Jurassic of UK are compositionally similar to those of Kota Formation, we conclude that Middle Jurassic age is a more reasonable estimate for the Kota Formation.

## Biogeographic Links of the Kota Vertebrate Fauna

Some of the well-known Jurassic continental vertebrate localities in the world are the Lower Jurassic Kayenta Formation, USA, the Middle Jurassic Kota Formation of India, the Middle Jurassic sites of U.K., the Middle Jurassic Cañadón Asfalto Formation of Argentina, the Middle Jurassic Isalo Group III of Madagascar, the Middle Jurassic Guelb el Ahmar site of Morocco (Haddoumi et al. 2016), the Upper Jurassic Morrison Formation of USA, the Upper Jurassic Tendaguru Beds of Tanzania, the Upper Jurassic Guimarota Lignite deposits of Portugal, and the Upper Jurassic Mugher Mudstone of Ethiopia (Goodwin et al. 1999). The Kota Formation has produced one of the richest continental Jurassic vertebrate faunas in Gondwana and with >42 taxa it represents a taxonomically diverse assemblage. All major groups of vertebrates are represented. Ostracods occur in great abundance and charophytes are also present though in limited numbers. The fauna is characterized by predominantly Laurasian taxa along with a few Gondwanan taxa. The Kota vertebrate fauna includes three taxa, viz., *Barapasaurus*, *Dyskritodon* and an australosphenidan which are restricted to the Gondwana in their distribution. *Barapasaurus tagorei*, a sauropod dinosaur from the Kota Formation is considered to be phylogenetically related to *Vulcanodon* of Zimbabwe. *Dyskritodon amazighi*, a eutriconodontid, was described from the Early Cretaceous Anoual Ksar Metlili site of Morocco, NW Africa (Sigogneau-Russell 1995). Later, Prasad and Manhas (2002) described a new species of this genus, *Dyskritodon indicus*, from the Kota Formation of India. Australosphenidan mammals are also restricted to the Middle Jurassic of Madagascar (Flynn et al.

1999) and South America (Rauhut et al. 2002; Martin and Rauhut 2005; Rougier et al. 2007), and Early Cretaceous of Australia (Rich et al. 1997, 2001). More recently, a definite lower molar and a possible upper molar of an australosphenidan mammal was recorded from the Kota Formation (Parmar et al. 2015). On the other hand, semionotid fishes, primitive ornithischian and dromaeosaurid dinosaurs, kuehneotheriid and amphiodontid symmetrodonts, morganucodontids, docodonts, possible dryolestids, multituberculates and yet to be described eleutherodontid haramiyidans are typical Laurasian taxa. None of these taxa are known from the Middle Jurassic Cañadón Asfalto Formation of Argentina and the Isalo Group III of Madagascar, and the Upper Jurassic Tendaguru Beds.

In the presence of primitive ornithischians (*Alocodon*-like, *Trimucrodon*-like), Dromaeosauridae indet., *Richardoestesia*-like, and multituberculate mammals, the fauna from the Upper Jurassic Guimarota Coal Mine is closely comparable to that of the Kota Formation. However, large theropod dinosaurs such as allosaurids and tyrannosaurids of the Guimarota fauna are missing in the Kota fauna. In fact at higher taxonomic levels, the vertebrate faunal composition of the Kota Formation comprising of freshwater hybodont sharks, semionotid fishes, amphibians, testudines, sphenodontids, crocodylians, pterosaurs, sauropod, primitive ornithischian and dromaeosaurid dinosaurs, symmetrodont, morganucodontid, eutriconodont, docodont, multituberculate mammals and eleutherodontid haramiyidans is more similar to that of English Bathonian localities such as the Upper Bathonian Forest Marble, Kirtlington Quarry (Evans and Milner 1994), the Middle Jurassic of Skye (Scotland) (Evans and Waldman 1996; Evans et al. 2006) and the Chipping Norton Limestone Formation at Hornsleasow Quarry, Gloucestershire (Metcalf et al. 1992; Metcalf and Walker 1994; Evans and Milner 1994) than to any other localities. Hence the Kota fauna broadly displays greater taxonomic affinities to the Laurasian British faunas rather than to Gondwanan faunas.

Among the Gondwanan faunas, the Moroccan Guelb el Ahmar site shares *Lepidotes*, Testudinata, rhynchocephalians, Atoposauridae crocodiles, pterosaur, theropod and ornithischian dinosaur remains with the Kota Formation (Haddoumi et al. 2016). Slightly younger ?Berriasian Ksar Metlili site also shares eutriconodont (*Dyskritodon*), multituberculates, and symmetrodonts, in addition to dromaeosaurids, ornithischians, pterosaurs, cryptodiran turtle, freshwater hybodont sharks, *Lepidotes* with the Kota Fauna. Even in the case of the Moroccan sites, the vertebrate fauna was considered to have close affinities with Laurasian British Bathonian faunas.

The predominantly Laurasian taxa in the Kota fauna implies that either these are the relict taxa with formerly

Pangaeian distribution or dispersed along a trans-Tethyan route across the Mediterranean Tethyan Sill as inferred for the Laurasian elements of Guelb el Ahmar fauna (Haddoumi et al. 2016). Haddoumi et al. (2016), while discussing the biogeographic relationships of supposedly Laurasian affinities of the Middle Jurassic Guelb el Ahmar biota, pondered over two possible biogeographic scenarios: 1) the taxa had Pangaeian distribution in the geological past and there are significant gaps in the fossil record of Gondwana; 2) the absence of Laurasian taxa reported from Guelb el Ahmar site in other Gondwanan Jurassic sites may represent real absences. The relatively restricted occurrence of the Kota fauna in other sites in Gondwana may also suggest provincialism or biogeographic partitioning within Gondwana. However, this lack of common fauna in the Gondwanan continents may also be the result of poor sampling in these areas as compared to Laurasia. Therefore, a clear picture would emerge as and when all the Jurassic sites of the southern hemisphere are extensively sampled for microvertebrate faunas.

## Conclusions

The Indian subcontinent has a unique history of being part of Gondwana that broke-up in the Late Jurassic and having subsequently drifted rapidly towards the north to collide with Asia in the Middle Eocene. The fauna from the Kota Formation, therefore, represents the fauna of pre-drift India and offers some insights into the biodiversity prior to the drift phase. Based on qualitative morphological observations of isolated teeth, five morphotypes of ornithischians, five morphotypes of Dromaeosauridae indet., one *Richardoestesia*-like form, and one morphotype of Theropoda indet. are identified in the vertebrate fauna of the Kota Formation. It adds at least five possible ornithischian and three theropod taxonomic groups to the existing record of two sauropod dinosaur taxa. Prior to this study no theropod dinosaurs have been reported from this formation and only the occurrence of ankylosaurids among the ornithischians have been documented so far. Although the morphotypes are identified at higher taxonomic levels, they point to greater diversity in the Jurassic dinosaur fauna of India. The close similarities between the vertebrate fauna of the Kota Formation and the Middle Jurassic deposits of UK favours a Middle Jurassic age for the Kota Formation. The predominant occurrence of Laurasian taxa over Gondwanan taxa underscores close biogeographic links between India and Laurasia with a restricted faunal interchanges between India and other Gondwanan landmasses in the Middle Jurassic. However, it may also be argued that many of these vertebrate groups had



a Pangaeian distribution and limited sampling in the Gondwanan continents obscures true intra-Gondwanan biogeographic relationships. A clear picture will emerge only when the Gondwanan Jurassic sites are extensively and intensively sampled.

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